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THE DEVELOPMENT OF THE WEBERIAN APPARATUS AND THE SWIM BLADDER IN THE CHANNEL CATFISH, ICTALURUS PUNCTATUS (RAFINESQUE)

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THE DEVELOPMENT OF THE WEBERIAN APPARATUS AND

THE SWIM BLADDER IN THE CHANNEL CATFISH,

ICTALURUS PUNCTATUS (RAFINESQUE)

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TABLE OF CONTENTS

THE DEVELOPMENT OF THE WEBERIAN APPARATUS AND THE SWIM BLADDER IN THE CHANNEL CATFISH, *ICTALURUS PUNCTATUS* (RAFINESQUE)

CHAPTER I

INTRODUCTION

Weber (1820), in his study of the skull and vertebrae in "*Cyprini carpionis*" and *Silurus glanis*, was the first to describe the modifications of the anterior vertebrae and the chain of ossicles which connect the auditory organ with the swim bladder. He concluded that the chain of ossicles functioned in hearing, named them auditory ossicles, and assigned the names claustrum, stapes, incus, and malleus to them.

Bridge and Haddon (1893) studied the gross morphology of these vertebrae and the related ossicles of 100 species of adult silurid fishes and introduced the names scaphium, intercalarium, and tripus into the literature as names for Weber's stapes, incus, and malleus, respectively. They named the chain of the four ossicles the "Weberian ossicles." By doing this they hoped simultaneously to honor Weber and to avoid confusing the origin of these with that of mammalian auditory ossicles.

In 1885, Sagemehl (fide Nelson, 1948) introduced the name Ostariophysi to include all the fishes that possess the auditory ossicles. Since the name Ostariophysi was established, the number of species included in the group has increased to more than 6,000 (Herald, 1961).

The representatives of Ostariophysi are found in the waters of North and South America, Europe, Africa, Asia, Australia, and Malagasay. Most species of this order are found in fresh water. According to Nikol'skii (1961), only two families of Ostariophysi are completely adapted to marine water. These belong to the suborder Siluroidei and are found in Australia and Malagasay.

Berg (1947) introduced the name Cypriniformes for Ostariophysi, dividing the order into four suborders: (1) Characinoidei, (2) Gymnotodei, (3) Cyprinoidei, and (4) Siluroidei. The first three of these suborders contain a total of about ten families while the fourth suborder contains approximately 28 families of catfishes (Herald, 1961).

Greenwood, et al. (1966) recognized eight superorders within the teleostean fishes. They grouped these eight superorders into three main divisions. Ostariophysi is considered a superorder belonging to Division III. This superorder is in turn divided into two orders, Cypriniformes and Siluriformes. In this study I follow this classification.

Since 1820 several papers have been published describing the Weberian apparatus in adult fishes for a single species or a group of species. Through the use of morphological differences in the Weberian apparatus Chranilov (1927, 1929) (fide Nelson, 1948) was able to

distinguish among the families of Cyprinidae, Cobitidae, and Siluridae. Nelson (1948) studied the comparative morphology of the Weberian apparatus of representatives of 16 catostomid genera. He was able to use the Weberian apparatus as a distinguishing criterion above the tribe level. Tilak (1963) constructed a taxonomic key using the Weberian apparatus as a reference source for identification of silurid fishes.

The literature concerning the studies of the Weberian apparatus has been reviewed by many writers. Notable among these are Bridge and Haddon (1893), Krumholz (1943), Nelson (1948), Karandikar and Masurekar (1954), and Niazi (1963).

The homology of the Weberian ossicles still concerns many workers in the field of comparative morphology. As stated by Bridge and Haddon (1893), the opinions of different investigators on the homology of the ossicles are based mainly upon comparative morphological studies of the condition and relationships of the ossicles in the less highly specialized Ostariophysi, principally the Cyprinidae. Table I shows the different views of several investigators. The different investigators agree that the Weberian ossicles are derived entirely from modified portions of the first three vertebrae. Bridge and Haddon (1893), however, stated that a satisfactory and final solution to the problems of the homology of these ossicles should be based on embryological study and that comparative anatomy alone is of little value.

Since 1820, the only published work on the embryological development of the Weberian apparatus in silurid fishes is that of Wright (1884) on Ictalurus (Ameiurus) catus and Mookerjee, et al. (1954) on Heteropneustes fossilis. Most of the work on the development of the

Weberian apparatus has been done on cyprinid fishes, e.s (minnows) of the order Cypriniformes. Notable among these are the following: Nusbaum (1908) on the carp, Cyprinus carpio; Matveiev (1929) on the rud, Scardinius erythrophthalmus; Watson (1939) on the goldfish, Carassius auratus; and Niazi (1963) on the fathead minnow, Pimephales promelas. Butler (1960) studied the development of the ossicles in the catastomid fish, the Rio Grande mountain sucker, Pantosteus plebius. These workers generally agree that the Weberian ossicles are derived in part from the anterior vertebrae and in part from the ossification of ligaments (Table II).

Because of the very close physiological relationship between the Weberian ossicles and the swim bladder in the Ostariophysi, it is important to study the development of both of these structures. The literature concerning the studies of the swim bladder in the adult bony fishes has been reviewed by many writers. Notable among these are the following: Bridge and Haddon (1893), McEwen (1940), and Jones and Marshall (1953).

The only published work concerning the morphology of the swim bladder in adult ictalurid fishes is that of Dobbin (1941). She studied the variations in the morphology of the swim bladder at the genus level and in some cases at the species level in the families occurring in New York and other eastern states.

In general the embryology of the swim bladder in bony fishes is well known, but still there are some variations between different species and, even in some cases, between congeners (Duwe, 1955). Among the workers in this field are: Tracy (1911) on the anchovy, Stolephorus

mitchilli; fundulus, Fundulus heteroclitus; menidia, Menidia menidia notata; toadfish, Opsanus tau; pipefish, Siphostoma fuscum; cunner, Tautogolabrus adspersus; and tautog, Tautoga onitis; Hoar (1937) on the Atlantic Salmon, Salmo salar; McEwen (1940) on Hemichromis bimaculata; Johnston (1953) on the largemouth black bass, Micropterus salmoides salmoides; Nelson (1959) on the common sucker, Catostomus commersoni, and Niazi (1963) on the fathead minnow, Pimephales promelas. In a search of the literature no work on the embryology of the swim bladder of ictalurid fishes could be found.

My study concerns the development of the Weberian apparatus and the swim bladder in the channel catfish, Ictalurus punctatus, one of the nine species belonging to the genus [family Ictaluridae, order Siluriformes, superorder Ostariophysi, Group III (Greenwood, et al., 1966)]. This fish is indigenous to many lakes and rivers of the United States and has been introduced into many others; its reported original range extends from the Great Plains region of Canada, and the southern part of the Hudson Bay drainage and the St. Lawrence Bay southward through the Great Lakes and the Mississippi valley (Moore, 1957).

CHAPTER II

MATERIALS AND METHODS

In this study adult, embryonic and larval stages were used. Adult fish were collected from Lake Texoma, Oklahoma. The total length was taken for each specimen at time of capture and the fish were stored frozen until preparation for study of the Weberian apparatus.

Several methods were used for the preparation of the Weberian apparatus in the adult. These methods can be divided into two groups. In the first group, the head of the fish was removed just posterior to the dorsal fin and either placed in boiling water or autoclaved to permit easy removal of the flesh. This method proved satisfactory for easy separation and study of the various components of the Weberian apparatus. The other methods include the use of X-ray, Alizarine red S, and the dissection of both frozen and fresh fish. The last three methods have the advantage of permitting the Weberian apparatus to be studied in its natural intact condition.

In order to obtain the various stages of development a pair of sexually mature channel catfish was kept in running water in a large glass aquarium at the U. S. Fish Hatchery at Tishomingo, Oklahoma. The female was injected with carp pituitary gland extract in order to induce ovulation. On 14 June 1964, between 2:00 and 5:00 PM, the pair began spawning. At 6:00 PM about 5,000 of the fertilized eggs were taken from

the aquarium and placed in an enclosure fashioned from small-mesh screen wire. The fertilized eggs within the enclosure were kept in running water at a temperature between 24 and 26 C. Samples of developing embryos were taken at 1-hr intervals for two days. The sampling period was gradually increased to intervals of 5 hr. On 20 June, the sixth day after fertilization, all the eggs were hatched. On 28 June, 1964, all larvae were transferred to the University of Oklahoma Biological Station, Lake Texoma. Here they were kept in two small aquaria in running lake water at a temperature varying between 24 and 29 C. Intervals between samples were increased from 5 to 8 hr by 1-hr steps.

On 19 July, 1964, 848 hr after fertilization, collecting was terminated. By this time the Weberian apparatus and the swim bladder were well developed. The larvae had attained an average total length of 28 mm.

The larvae were fed ground beef liver or commercial trout food four times daily from 7:00 AM to midnight at intervals of about 5 hr. Samples were always taken just before feeding to avoid having food in the gut of the sectioned larvae.

The samples taken at each stage were in most cases fixed in three different fixatives: Bouin's fluid, Smith's fixative, and F.A.A.

Dioxane was used for dehydration, and Fisher Tissuemat was used for embedding the embryos and larvae. Transverse, sagittal, and frontal serial sections of selected stages were made. Sections were cut between 5 and 10 μ in thickness. The sections of the embryos and young larvae were stained with Harris haematoxylin and eosin or Delafield's haematoxylin and eosin. Mallory's triple stain proved to be satisfactory

for the older stages only. All sections were studied under a compound microscope.

Drawings of the Weberian apparatus elements of the adult were made either by free hand sketching from the prepared bones or by tracings from enlarged photographs. The photomicrographs were taken with a Carl Zeiss camera mounted on a monocular petrographic Carl Zeiss compound microscope.

CHAPTER III

WEBERIAN APPARATUS

The Morphology of the Weberian Apparatus in the Adult

The Weberian apparatus consists of two functional units, the pars sustentaculum, and the pars auditum (Nelson, 1948).

Pars sustentaculum

This unit consists of the nonmovable parts of the first four vertebrae (Plates I-IV). The first vertebra is small and free while the other three are completely fused to form, collectively, a single unit called the "complex vertebra." These four vertebrae are the supporting and protecting unit of the pars auditum.

The First Vertebra (Plate V, Figs. 1, 2, and 3)

This vertebra is slightly amphicoelous, the anterior and posterior concavities having the same depth. The vertebra is greatly modified by the loss of the neural spine and the transverse processes. Ventrally, it carries two small basapophyses (BP), one on each side. Its neural arches, derived from the first pair of basidorsals, are also greatly modified, and form part of the scaphia.

On the ventral side of the centrum of this vertebra is a large median depression (MD). Bordering this depression laterally, are two, posteriorly projecting, laminar, articulating processes (VARP) from

the basapophyses. These laminar, articulating processes interlock with similar processes directed anteriorly from the ventrolateral sides of the superficial bones of the complex vertebra (APSB, Plate IV, Fig. 2).

On the dorsolateral surface of the first vertebra there are two small, cup-shaped depressions (DP, Plate V, Figs. 1 and 3) into which fit the condylar processes of the right and left scaphia. The upper surfaces of the centrum of the first vertebra (C_1) and the basioccipital (BOC, Plate V, Figs. 4, 5, and 6) are slightly lower than those of the centra of the other vertebrae and the horizontal plate (HP) of the exoccipitals (Plate V, Figs. 4 and 6). The horizontal plate (HP, Plate V, Figs. 4 and 5) separates the foramen magnum (FM) from the cavum sinus imparis (CSI) in the occipital region of the skull. There is a small pad (PD, Plate V, Figs. 6 and 7) of fibrous connective tissue lying above the centrum of the first vertebra between the scaphia. This pad extends anteriorly, above the posterior end of the basioccipital and fuses with the dorsoposterior median edge of the horizontal plate (Plate V, Figs. 6 and 7). This fusion, which occurs only at the middle edge of the horizontal plate, leaves an atrial cavity on each side of the pad (ASI, Plate V, Fig. 7). This pad is the thickest part of the epineural tube in this region.

The functions of this pad and the epineural tube, as far as this morphological study indicates, are:

(1) Separation of the right atrium sinus imparis from the left.

(2) Support to both the scaphia and the claustra and limitation of their movements.

(3) Support for the spinal cord.

The anterior margin of the centrum of the first vertebra is strongly attached to the posterior margin of the concave basioccipital of the skull through the intervertebral ligament and the persistent notochord existing between them plus the mesenchymatous tissue surrounding both the basioccipital and the first centrum.

The Complex Vertebra (C_{2-3-4}; Plate II, Fig. 2; and CC′, Plate IV, Fig. 2.)

This structure was described by Weber (1820) as the second vertebra in the wels, Silurus glanis. The presence of the spinal ganglia and the study of its development indicate that there are three vertebrae within this complex vertebra. The fifth vertebra is united but not rigidly fused with the complex vertebra. In this work, the fifth vertebra is not included with the pars sustentaculum since it does not support, protect, or contribute to the Weberian ossicles.

The centrum of the complex vertebra is strongly amphicoelous, the concavity being narrower and deeper on the posterior end. The anterior concavity of the centrum of this vertebra represents morphologically the concavity of the second vertebra, while the posterior one is homologous with that of the fourth vertebra. Apparently the centrum of the third vertebra lost both concavities during ontogeny. Karandikar and Masurekar (1954) observed this in Arius platystomus too. No intervertebral ligaments or swollen areas exist between the second and third, or between the third and fourth centra.

The ventrolateral sides of this vertebra are invested by two superficial bones (SB, Plate II, Fig. 2 and Plate IV, Fig. 2), one on each side. Each superficial bone extends forward and gives rise to the

ventrolateral lamellar processes (APSB, Plate IV, Fig. 2) which interlock with those (VARP) of the first vertebra. Posteriorly, the superficial bone extends as far as the posterior end of the fifth centrum (C_5) and meshes with grooves located on the ventrolateral sides of the fifth centrum (Plate IV, Fig. 2). Ventrally, each superficial bone extends vertically downwards forming a long bony ridge (BR, Plate II, Fig. 2) along each side of the bottom of the complex centrum and the centrum of the fifth vertebra. These bony ridges are homologous with the basapophyses of other vertebrae. These two basapophyses are the lateral walls of the subcentrum aortic groove (AOG, Plate II, Fig. 2). Dorsally, the superficial bone of each side forms a shelf which supports the postcardinal vein on each side (CDG, Plate IV, Fig. 2). There are two lateral ridges (LR, Plate II, Fig. 2 and Plate IV, Fig. 2), one on each side of the anterolateral part of the complex centrum. These ridges provide for the attachment of the swim bladder from its anterior end.

The transverse processes which originate from the basiventrals of the complex vertebra are greatly modified. They are missing from the second vertebra, and modified into tripodes (plural of tripus) on the third vertebra. Those of the fourth vertebra are greatly enlarged. These are completely fused to the neural arch and the base of the neural spine of the complex vertebra anteriorly and the dorsolateral sides of the centrum of the complex vertebra posteriorly (P_4A and P_4P, Plate II, Figs. 1 and 2). The transverse process of the fourth vertebra has two pairs of expansions:

(1) Large anterolateral pair (P_4A) which is curved sharply downward and slightly backward (Plate III, Figs. 1 and 2). At the

anterolateral side of each expansion, there is an oval articulating facet which articulates with a similar facet on the ventral arm of the posttemporal bone ($ARTP_4$, Plate IV, Fig. 1);

(2) The posterolateral expansions (P_4P) are much thinner and more horizontal than the anterolateral pair. The outer margins of the posterolateral expansions are longer, thicker and higher than the inner margins which are fused to the upper sides of the posterior half of the centrum of the complex vertebra (Plate II, Fig. 1 and Plate III, Fig. 2).

There are two pairs of semicircular notches, one on each side of the transverse process of the fourth vertebra (Plate II). The anterior pair (NTA) is larger than the posterior pair (NTP) and it is located between the anterolateral and the posterolateral expansions of the transverse process of the fourth vertebra. The posterior pair is located between the posterolateral expansions of the fourth vertebra and the transverse process of the fifth vertebra (P_5). The transverse process of the fifth vertebra is united, but not fused, with that of the fourth vertebra (Plate II). The suture between the two transverse processes can be seen clearly in the dried skeleton.

From the ventral surface of the posterolateral expansions of the fourth transverse process, near its connection with the process of the fifth vertebra, a ribbon-like, bony process called the "dorsal lamina" extends anteromesially between the crescentic process of the tripus and the postcardinal vein (DL, Plate II, Fig. 2). The dorsal lamina terminates in the radial nodule (RN) which is attached to but not fused with the superficial bone of the complex centrum on each side. The radial nodule is surrounded posteriorly by the crescentic process

of the tripus (TR.C, Plate II, Fig. 2 and Plate III, Fig. 2) and connected to it by the radial fibers (RF). The radial nodule, part of the dorsal lamina, and the crescentic process are embedded in the tunica externa of the swim bladder. Both the dorsal lamina and the radial nodule constitute the os suspensorium.

The neural arches of the second, third, and fourth vertebrae are fused, and completely surround the spinal cord along the dorsal side of the complex centrum except in two areas located underneath the anterior expansions of the transverse processes of the fourth vertebra near its connection with the neural arch of the third. From the shape of these openings, I shall refer to them as "oval slits." These two oval slits (OS, Plate IV, Fig. 2) are parallel to the anterior edges of the neural arch of the second vertebra and serve for the articulation of the articulating processes of the tripodes. This observation has not been reported by previous workers who have studied the osteology of silurid fishes.

There are only two neural spines which belong to the complex vertebra. These are of the third and fourth vertebrae. Apparently the second vertebra has lost its neural spine. The neural spine of the third vertebra (NS_3, Plate II, Fig. 1, Plate III, Figs. 1 and 2 and Plate IV, Fig. 2) bifurcates at the tip and articulates with the supra-occipital. The neural spine of the fourth vertebra (NS_4) is inclined posteriorly and is also bifurcated at its tip. The bifurcation of the neural spine of the fourth vertebra is deeper, wider, and thicker than that of the third neural spine. The neural spines of the third and fourth vertebrae are connected by a median, vertical, curved, bony plate

(VRN, Plate II, Fig. 1, Plate III, Fig. 2 and Plate IV, Fig. 2). The tip of the neural spine of the fourth vertebra extends backward and ends above the posterior end of the centrum of the fifth vertebra (Plates I through IV).

Pars Auditum

This unit consists of two chains of ossicles, one on each side of the first four vertebrae. Each chain is made of four ossicles. Beginning anteriorly they are, the claustrum (CL), Scaphium (SC), intercalarium (IN), and tripus (TR). Except for the claustrum, the ossicles are interconnected by a ligament (interossicular ligament), and they join the auditory organs with the swim bladder.

Claustrum, (of Weber, 1820; Muller, 1853; Bridge and Haddon, 1893; Hinlage of Thilo, 1908)

The claustrum (CL, Plate III, Fig. 2; Plate IV, Fig. 1 and Plate VI, Figs. 1 and 2) is a small triangular bone. It is thin except for a thickness along the posterior edge. It is slightly convex laterally and concave mesially. The whole ossicle on each side is embedded in the fibrous connective tissue connecting the posterior edge of the exoccipital bone with the anterior edge of the neural arch of the complex vertebra. Dorsally, the claustrum is connected to the cartilaginous tissue above it (CART, Plate IV, Fig. 1). On its anterior surface the claustrum is joined to the exoccipital bone (EXO, Plate IV, Fig. 1) by fibrous connective tissue. The ventral and posterior edges of the claustrum are surrounded by the horizontal process (SC.H, Plate V, Fig. 1) and the ascending process (SC.A) of the scaphium, respectively.

This ossicle forms a very small portion of the upper, outer wall of the atrium sinus imparis; there is no structural relationship between it and any vertebra.

Scaphium, (of Bridge and Haddon, 1893; Stapes of Weber, 1820; Steighugel of Muller, 1853; and Deckel of Thilo, 1908).

The scaphium (SC, Plate III, Fig. 1, and Plate VI, Figs. 5 and 6) lies immediately posterior to the claustrum, surrounding it on its ventral and posterior edges. It consists of three processes (Plate V, Fig. 1 and Plate VI, Figs. 5 and 6), a condition similar to that described for Amiurus (=Ameiurus, Ictalurus) catus by Wright (1884):

(1) An anterior horizontal process (SC.H, Plate VI, Figs. 5 and 6), concave mesially and convex laterally, lies between the dorsolateral edge of the centrum of the first vertebra and the ventral edge of the claustrum (Plate V, Fig. 1). It terminates on the posteroventral surface of the exoccipital (RSC.H, Plate IV, Fig. 1), at its inner margin. The inner concave surface forms the outer wall of the atrium sinus imparis (ATSI, Plate VI, Fig. 7). Its outer convex surface has a small, flat area (ALS, Plate VI, Fig. 5) serving as an attachment for the inner end of the interossicular ligament (IL, Plate VI, Fig. 7). This flattened area is more prominent in larger fishes;

(2) The ascending process (SC.A, Plate V, Fig. 1 and Plate VI, Figs. 5 and 6) is perpendicular to the anterior horizontal process and lies immediately lateral and anterior to the neural arch of the second vertebra (NA_2, Plate III, Fig. 2). The ascending process and the condylar process serve as a hinge for the lateromesial motion of the horizontal process. The ascending process is broadest near its base where

it joins with the other two processes. This process is embedded in the fibrous connective tissue surrounding the edge of the foramen magnum and extends on each side posteriorly to the anterior margin of the neural arch of the complex vertebra;

(3) The short, globular and cartilaginous condylar process (SC.C, Plate V, Fig. 1 and Plate VI, Figs. 5 and 6) articulates with a pit (DP, Plate V, Figs. 1 and 3) located on the dorsolateral surface of the centrum of the first vertebra, and permits only lateral movement of the horizontal process.

Intercalarium, (of Bridge and Haddon, 1893; Incus of Weber, 1820; Ambos of Mullar, 1853; and Lenker of Thilo, 1908).

The intercalarium (Plate VI, Figs. 3, 4, and IN, Fig. 7) is a small, irregularly cylindrical ossicle, embedded in the interossicular ligament (IL, Plate VI, Fig. 7) between and perpendicular to both the anterior horizontal process of the scaphium and the inner anterior end of the tripus. There is no connection between this ossicle and any vertebra in the adult.

Tripus, (of Bridge and Haddon, 1893; Malleus of Weber, 1820; Hammer of Mullar, 1853; and Hebel of Thilo, 1908).

The tripus (TR, Plate II, Fig. 2; Plate VI, Fig. 7; and Plate VII, Figs. 1, 2, and 3) is the largest ossicle in the Weberian series. It is flattened dorsoventrally, and its edges face inward and outward with regard to the vertebral column. This ossicle is divided into three processes: the anterior process (TR.A), the articular process (TR.ART), and the crescentic process (TR.C).

(1) The anterior process lies alongside and parallel to the anterior part of the complex centrum and the centrum of the first vertebra (TR.A, Plate III, Fig. 1). The inner edge of this process is thicker than the outer edge. The tip of the process has a notch (AIL, Plate VII, Figs. 2 and 3) on its anterior inner side which faces the middle convex side of the scaphium. The interossicular ligament (IL, Plate VI, Fig. 7) connects this notch with a facet (ALS, Plate VI, Fig. 5) on the convex side of the scaphium.

(2) The thin flattened crescentic process is a posterior continuation of the anterior process. It is C-shaped and bends inward upon itself. Most of this process is embedded in the tunica externa of the anterior chamber of the swim bladder. This process encircles the radial nodule (RN, Plate II, Fig. 2 and Plate III, Fig. 2) and is connected to it by the radial fibers (RF).

(3) The triangularly shaped articular process is formed at the junction of the first two processes. This process articulates with the neural arch of the complex vertebra through the oval slit (OS, Plate IV, Fig. 2).

The tripus is freely movable laterally on its articulation with the neural arch of the complex centrum by means of the articular process.

The Development of the Weberian Ossicles

The following stages show the development of the Weberian ossicles from the time they appear until the time they represent the adult condition.

10.4 mm larva, 152 hr after fertilization (Plate VIII, Figs. 1-6)

In this stage the first four pairs of basidorsals (BD_{1-4}), associated with the anterior portion of the notochord, are developing, their sizes gradually decreasing posteriorly to anteriorly. The first pair of basidorsals is still in the procartilaginous stage, while the other three pairs have progressed to the cartilaginous stage. There is no direct connection between the first pair of basidorsals and the elastica externa of the notochord, although the bases of the other three pairs fuse with it.

Two pairs of basiventrals are associated with the notochord in the region where the third and fourth vertebra will be formed. These two procartilaginous basiventrals are located immediately anterior and ventrolateral to the third and fourth basidorsals respectively.

By now, although the portions of the Weberian ossicles that form from cartilage are developed, there is as yet no indication of the condensed mesenchymal cells also contributing to their formation.

11.1 mm larva, 170 hr after fertilization (Plate IX, Fig. 1)

In this stage the first four pairs of basidorsals and the two pairs of basiventrals are in the cartilaginous stage. An aggregation of mesenchymal cells lies along the anterior side of the first pair of basidorsals (SC.H, Fig. 1).

12.1 mm larva, 194 hr after fertilization (Plate IX, Fig. 2)

As the larva grows, the form of the Weberian ossicles and the related parts of the Weberian apparatus become clearer. In this stage the ventral portion of the aggregated mesenchymal cells, anterior to the

first basidorsal and mentioned in the last stage, condenses and starts to ossify (SC.H, Fig. 2). Ossification of the mesenchymal cells starts from the central portion of the distal part of the aggregation and proceeds posteriorly toward the basidorsal of the first vertebra. The ossified mesenchymal cells form the rudiment of the horizontal process of the scaphium. In this stage there are two new groups of condensed mesenchymal cells appearing on each side. The first group is lateral to the second basidorsal (MI, Fig. 2), while the second group is antero-lateral to the basiventral of the third vertebra (not shown in Fig. 2). The distal portion of the first new condensed nesenchymal cells shows signs of ossification and constitutes the beginning of the manubrium incudis of the intercalarium. The mesenchymal cells between the rudiment of the manubrium incudis and the rudiment of the horizontal process of the scaphium elongate and arrange themselves in the form of a band. This band is the beginning of the ligumentum scaphium. The second new group of condensed mesenchymal cells that appears in this stage is the beginning of the epipleural rib of the third vertebra which contributes later to the formation of the anterior process of the tripus (not shown in Fig. 2).

12.3 mm larva, 200 hr after fertilization (Plate IX, Figs. 3-6)

The following conditions exist at this stage:

(1) The claustrum is still in the mesenchyme stage.

(2) The rudiment of the horizontal process of the scaphium is more ossified (SC.H, Figs. 3 and 4).

(3) The manubrium incudis of the intercalarium is well ossified.

It is connected with the basidorsal of the second vertebra through the shaft which can be seen in this stage (Figs. 3 and 4).

(4) Part of the condensed mesenchymal cells anterolateral to the basiventral of the third vertebra are ossified (TR.A, Figs 3 and 4).

(5) The ligamentum scaphium continues to grow posteriorly to join the distal portion of the basiventral of the third vertebra. The portion of the ligament between the manubrium incudis and the distal portion of the basiventral of the third vertebra is the ligamentum tripus. Both the ligamentum scaphium and the ligamentum tripus form the interossicular ligament. In this stage another ligament starts to develop through the aggregation and elongation of the mesenchymal cells which are between the distal portion of the basiventrals of the third and the fourth vertebrae (IBL, Figs. 4 and 5).

(6) The distal portion of the basiventral of the third vertebra is embedded in the tunica externa of the swim bladder (BV_3, Fig. 6).

(7) The radial nodule on each side appears in this stage as an ossified knob on the ventrolateral side of the notochord at the level of the basiventral of the third vertebra (RN, Fig. 6). Each knob is connected with the ventral side of the basiventral of the fourth vertebra through a band of mesenchymal cells. This band is the rudiment of the dorsal lamina (DL, Fig. 6). Starting from the radial nodule, the band proceeds posterodorsally between the postcardinal vein from the inside and the basiventral of the third vertebra from the outside. Both the radial nodule and the rudiment of the dorsal lamina are embedded in the tunica externa of the swim bladder.

(8) The pleural rib of the fourth vertebra (P_4) starts to develop as a direct ossification from the anterodistal portion of the basiventral of the fourth vertebra. This ossification proceeds anterolaterally toward the postcleithrum, pushing the muscles in front of it.

Larval stages at 13.0 mm, 13.5 mm, 13.7 mm; 224, 237, 245 hr after fertilization respectively (Plates X, XI, and XII respectively)

The channel catfish larvae in these three stages were serially sectioned in the three different major planes. These are the stages that are best for determining the homologies of the Weberian ossicles. For convenience each ossicle will be discussed separately.

Claustrum:

The claustrum rudiment is still in the condensed mesenchymal stage in a larve of 224 hr (13.0 mm). The posterior edge of this rudiment thickens and is in the procartilaginous stage in a larve of 237 hr (13.5 mm). The procartilaginous portion is condrified in a larva of 245 hr (13.7 mm).

The claustrum in these three stages occupies the same position and has almost the same general shape as that of the adult. It is embedded in the fibrous connective tissue, surrounding the spinal cord in the region of the first vertebra, between the basidorsal of the first vertebra and the lateral cartigalinous mass of the occipital region (CL, Plate X, Fig. 2; Plate XII, Fig. 1). The claustrum is surrounded dorsally by the dorsal cartilaginous mass of the occipital region and ventrally by the horizontal process of the scaphium (CLO and CL, Plate XI, Figs. 1 and 2). The claustrum in these larval stages as well as in

the adult, forms the upper part of the outer wall of the atrium sinus imparis; and has no direct connection with the other Weberian ossicles.

Scaphium:

The development of the scaphium in these larval stages is completed. It occupies the same position and has the same shape as that of the adult. It consists of the spoon-shaped ossified horizontal process (SC.H, Plate X, Figs. 2 and 3; Plate XI, Fig. 1, and Plate XII, Figs. 2, 4, and 5), and the cartilaginous first basidorsal [SC (BD_1), Plate X, Fig. 2; BD_1(SC) Plate XI, Fig. 2 and BD_1 Plate XII, Fig. 2]. The horizontal process is concave from the inner side and convex from the outside (SC.H, Plate XI, Fig. 1). Its central portion is ossified while its outer and inner portions are still in the mesenchymal stage. The concave side forms the lateral outer wall of the atrium sinus imparis, the inner wall of the atrium sinus imparis being formed by a thick pad of fibroconnective tissue (endorhachis) which separates the right atrium sinus imparis from the left one. The horizontal process lies between the ventral edge of the claustrum and the dorsolateral sides of the first segment of the notochord and the posterodorsolateral portion of the basioccipital bone of the skull. The midportion of the outer convex side of the horizontal process serves for the attachment of the ligamentum scaphium.

The portion of the first basidorsal below the junction of the horizontal process is the condylar process of the scaphium (SC.C Plate X, Fig. 3 and Plate XII, Fig. 5), while that portion above the junction of the horizontal process is the ascending process (SC.A, Plate XI, Fig. 3).

The condylar process (SC.C, Plate X, Fig. 3 and Plate XII, Fig. 5) articulates with the anterior segment of the notochord through a concavity located on the dorsolateral side of the segment. This articulation permits the horizontal process of the scaphium to move outward and inward. The basidorsal of the first vertebra in these stages is not perpendicular to the notochord as are those of the other basidorsals; it is slightly slanted posteriorly. Its distal portion is above the level of the second basidorsal [SC (BD_1), Plate X, Fig. 2 and SC.A, Plate XI, Fig. 3].

Intercalarium:

The intercalarium in these stages has the same shape and location as that of adult cyprinid fishes. It can be divided into three processes, the ascending process, the descending (articular) process and the horizontal process.

The ascending process is very short, and is the dorsal portion of the second basidorsal above the junction of the horizontal process.

The descending process is the thickest; it is long, immovable and completely fused with the elastica externa of the notochord (BD_2, Plate X, Fig. 2 and Plate XI, Fig. 3).

The horizontal process develops from a direct ossification of mesenchymal cells like the horizontal process of the scaphium. It is the longest and the narrowest process; and is directed anterolaterally with its distal portion (i.e., the manubrium incudis) embedded in the interossicular ligament [MI (IN), Plate X, Fig. 4 and MI, Plate XII, Fig. 4] while the rest of it (the shaft) is narrow and rounded (S, Plate XI, Fig. 3 and Plate XII, Fig. 4).

Tripus

In these stages part of the ligamentum tripus ossifies and then fuses with the epipleural rib of the third vertebra. Both unite to form the anterior process of the tripus (TR.A, Plate XI, Figs. 2 and 3 and Plate XII, Figs. 4 and 5). In these stages the distal portion of this process still has not reached the level of the midportion of the horizontal process of the scaphium. The portion of the ligamentum tripus, not ossified, is equal in length to the ligamentum scaphium. The dorsodistal portion of the basiventral of the third vertebra is connected through the interbasiventral ligament with the ventrodistal portion of the basiventral of the fourth vertebra. The pleural rib of the fourth vertebra is elongated and grows more anterolaterally towards the postcleithrum, pushing the muscles in front of it. The basiventral of the fourth vertebra and its pleural rib (P_4, Plate X, Fig. 6; Plate XI, Figs. 4 and 5, and Plate XII, Figs. 4 and 5) border the saccus paravertebralis posteriorly and dorsally. All the Weberian ossicles are located within this space which probably gives them more freedom for movement. The dorsal lamina is ossified in these stages (DL, Plate XI, Fig. 5).

15.7 mm larva, 346 hr after fertilization (Plate XIII, Figs. 1-6)

There is little advancement in this stage over the other three stages.

(1) The claustrum with its two components (i.e., the cartilaginous portion and membranous portion) is well developed (CL, Fig. 3).

(2) The horizontal process of the scaphium is well ossified (SC.H, Figs. 1 and 2).

(3) The fibroconnective tissue pad which separates the left atrium sinus imparis from the right one is more compact (ER, Figs. 2 and 3).

(4) The basidorsals of the second vertebra are in the degeneration stage. They will be replaced by membranous bone (BD_2, Fig. 4).

(5) The horizontal process of the intercalarium is directed more anteriorly than laterally. It still consists of the manubrium incudis (MI, Fig. 2) and the shaft (S, Figs. 3 and 4).

(6) The anterior process of the tripus is well ossified and still has not reached the level of the midportion of the horizontal process of the scaphium (TR.A, Figs. 3 and 4).

(7) The basiventral of the third vertebra is now degenerating and is to be replaced by bone to form the articulating and crescentic processes (BV_3, Fig. 5).

(8) The interbasiventral ligament connects the distal portions of the basiventrals of the third and the fourth vertebra (IBL, Fig. 6). The connections are with the dorsal surface of the third and the ventral surface of the fourth vertebra.

36 mm juvenile: (Plate XIV, Figs. 1-6)

Advancement over the previous stages:

(1) The ventral portion of the cartilaginous element of the claustrum is ossifying in this stage (CL, Fig. 2).

(2) Except for the condylar process (SC.C, Fig. 4) the whole scaphium is ossified.

(3) Except for the manubrium incudis [MI(IN), Fig. 1] embedded in the interossicular ligament (IL, Fig. 2), the whole horizontal process of the intercalarium (i.e., the shaft) has disappeared.

(4) The anterior process of the tripus is well ossified and extends anteriorly to the level of the middle portion of the horizontal process of the scaphium (TR.A, Fig. 1).

(5) The crescentic process (TR.C, Fig. 6) and the articulating process (TR.AR, Fig. 5) of the tripus which developed in the earlier stages has been replaced with bone. The dorsal portion of the articulating process has developed directly from ossified mesenchyme and articulates with the neural arch of the third vertebra through the "oval slit" (TR.AR, Fig. 5).

(6) The crescentic process is embedded in the tunica externa of the swim bladder (TR.C, Fig. 6).

(7) The interbasiventral ligament (IBL, Fig. 5) joins the dorsal surface of the tripus near the articular process with the ventral side of the parapophysis of the fourth vertebra. This ligament gives more support to the tripus and reduces its movement.

(8) The neural arches are completely replaced by bone and those of the second, third, and fourth are united to form the neural arch of the complex vertebra.

(9) The basiventral of the fourth vertebra, after it has been replaced by bone, together with its pleural rib forms the parapophysis which is greatly enlarged in this stage. It is growing anterolaterally and articulates with the postcleithrum. At the same time the parapophysis grows inward and outward. Its inward growth fuses with the neural arches

starting posteriorly and proceeding anteriorly (P_4A, Fig. 4).

(10) The four Weberian ossicles are occupying the saccus paravertebralis (SPV, Fig. 3).

(11) The dorsal lamina is well developed with its radial nodule (DL, Fig. 6).

The Development of the Pars Sustentaculum

The development of the teleost vertebral column has been studied in detail by many workers notably, Ramanujam (1929), MacBride (1932), Faruqi (1935), and Mookerjee, et al. (1940). My study is restricted to a brief description of the development of the first four vertebrae (i.e., the pars sustentaculum) in the channel catfish.

9.5 mm larva, 123 hr after fertilization (Plate XV, Figs 2 and 3)

(1) In this stage the notochord consists of two morphologically distinct types of cells: large, vacuolated cells (NT.V, Fig. 3), occupying the entire central portion of the notochord; and small, nonvacuolated peripheral notochordal cells (NT.P, Fig. 3), surrounding the first cell type.

(2) The single-cell layer of peripheral notochordal cells is surrounded by a noncellular (cuticular) membrane called the elastica externa (EE, Fig. 3).

(3) Sclerotomic cells migrate from the sclerotome of each somite, aggregating around the elastica externa and form the perichordal sheath primordium (PSP, Fig. 3).

(4) The sclerotomic cells, previously aggregated in the earlier stages into areas where the basidorsals and basiventrals would

later form, exist in this stage as either condensed mesenchymal cells or procartilaginous cells.

(5) The notochord in this stage is cylindrical. There are no segmental spaces between the peripheral notochordal cells and the elastica externa (Fig. 1).

(6) The first pair of basidorsals and the basiventrals of the future third and fourth vertebrae are in the condensed mesenchymal stage.

(7) The second, third, and fourth pairs of basidorsals are in the procartilage stage. Their distal portions are still below the level of the upper surface of the spinal cord.

(8) One pair of spinal ganglia is associated with each pair of myotomes.

12.7 mm larva, 218 hr after fertilization (Plate XV, Figs. 5-6)

(1) The sclerotomic cells, aggregated around the elastica externa in the last stage, condense and begin forming the perichordal sheath in this stage (PS, Fig. 6).

(2) The perichordal sheath cells and the peripheral notochordal cells are more thickened opposite the midmyotomal regions than in the mysoeptal regions (Fig. 4).

(3) Between the thickened peripheral notochordal cells and the elastica externa, spaces have formed. These spaces delineate the intervertebral regions which also face the midmyotomes. The regions facing the myosepta and occupying those areas between two successive, thickened, perichordal sheath cells are the vertebral regions.

(4) The sclerotomic cells located on the lateral sides of the dorsal aorta are more condensed in this stage (Figs. 5 and 6).

(5) There is an outgrowth from the midventral side of the anterior portion of the perichordal sheath. This outgrowth presses on the dorsal surface of the dorsal aorta giving it a cordate shape when viewed in a transverse section (Figs. 5 and 6).

(6) The basidorsals and the basiventrals mentioned in the last stage are all cartilaginous. The third and fourth basidorsals have elongated and have fused dorsally and dorsolaterally above the spinal cord. This fusion was observed for the first time in the larva of 200 hr (12.3 mm).

(7) There is a fusion of the bases of the second through the fourth pairs of basidorsals and the third through the fourth pairs of basiventrals to the elastica externa, although there is no direct connection between the first pair of basidorsals and the elastica externa.

(8) The spinal ganglia are larger than before.

20.0 mm larva, 600 hr after fertilization (Plate XV, Figs. 8-9)

(1) In the unmodified vertebrae the perichordal sheath, with the exception of the intervertebral regions, is ossified, joining the elastica externa to form the vertebral centrum.

(2) The thickened perichordal sheath in the intervertebral region is named the intervertebral ring (IVR, Fig. 7). The elastica externa in this region becomes very thin, finally losing its structural identity (Fig. 7).

(3) The thickened peripheral notochordal cells and the thickened perichordal sheath between the second and third and the third

and fourth vertebrae have failed to complete their development. There are no spaces or dilations between the vertebral regions (Fig. 7). As a result of the failure of separation of the second, third and fourth vertebrae, the complex vertebra is formed (Fig. 7).

(4) In the unmodified vertebrae another notochordal sheath (i.e., elastica interna) forms between the thickened peripheral notochordal cells and the elastica externa (EI, Figs. 7 and 9).

(5) The axial septum (AS, Figs. 7 and 9) and the transverse septa (ICS, Fig. 7) are well developed. I suggest calling the transverse septum, located in the middle of each future vertebra, "the intracentral septum." These septa indicate the number and level of the basidorsals.

(6) In this stage the tunica externa of the swim bladder has come into contact with the second, third and fourth future vertebrae (SB.TE, Fig. 7).

(7) The longitudinal outgrowth from the midventral surface of the anterior portion of the perichordal sheath, whose formation began in the last stage, is well developed, almost dividing the lumen of the dorsal aorta into right and left portions (Figs. 8 and 9).

(8) The connective tissue, bounding the dorsal aorta laterally, in the last stage, is ossified in this stage. This is the beginning of the subvertebral canal wall.

(9) The first four pairs of basidorsals are well ossified, with the exception of the bases of the first pair which are the condylar processes of the scaphia. The neural arches of the components of the complex vertebra are completely united to form the common neural arch

except that the oval slits remain to serve for articulation of the tripodes. The neural spines of the third and fourth vertebrae are united through the vertical ridge.

(10) The basiventrals of the third vertebra give rise to the tripodes. Those of the fourth contribute to the fourth parapophysis in the following manner: A connective tissue overlying, but not continuous with the connective tissue surrounding the swim bladder, extends in a continuous sheet anterolaterally and posterolaterally between the fourth pair of basiventrals and their pleural ribs. As this sheet ossifies, it fuses with the ossifying fourth vertebral basiventrals and with their pleural ribs, which extend anterolaterally from the anterodistal faces of each fourth basiventral. The fusion of these three, now ossified components, forms a broadly ossified sheet overlying the swim bladder and extending anterolaterally and posterolaterally from the main body of the complex vertebra. This sheet eventually fuses to the neural arch of the complex vertebra and is usually referred to as the parapophysis of the fourth vertebra. The epipleural ribs of the fourth vertebra begin ossification immediately lateral to the third centrum and grow posterodorsolaterally to join the fourth basiventral on its ventrodistal surface. This ossification remains distinct in the adult and is known as the radial nodule and the dorsal lamina.

Discussion

Homology of the Weberian ossicles

Watson (1939), Mookerjee, et al. (1954), Butler (1960), and Niazi (1963) recorded that there are three general theories concerning

the origin and homology of the Weberian ossicles (i.e., pars auditum). Weber (1820), the first to describe these ossicles in Silurus glanis and "Cyprini carpionis", homologized them with the ear ossicles of mammals and named them claustrum, stapes, incus, and malleus. Comparative anatomists who did not agree with Weber's homology, believed that these ossicles were derived mainly from the first three or four vertebrae (Table I). Embryological studies proved that these ossicles were derived in part from the anterior vertebrae and in part from connective tissue ossifications (Table II).

Claustrum: (Tables I and II)

Many workers believed that the claustrum is a modified neural spine of the first vertebra, but Hora (1922) believed that it is a modified neural arch of the first vertebra. Grassi (1883) was of the opinion that this ossicle is derived from the occipital region of the skull. Watson (1939) agreed with Kindred (1919) that the claustrum represents an intercalated structure. Butler (1960) and Niazi (1963) who found the origin of this ossicle failed to homologize it.

In the channel catfish the claustrum is formed by the fusion of two separate components, the thick posterior edge from cartilage, and the anterior thin portion from membrane bone. The entire ossicle is located between the first postvagal nerve (i.e., the first spinal nerve or the occipital spinal nerve) and a small additional spinal nerve. The latter nerve emerges between the claustrum and the ascending process of the scaphium. It was observed by Sagemehl (1885) in Silurus glanis (fide Wright, 1885 and Bridge and Haddon, 1893). Wright (1885) and Bridge and Haddon (1893) failed to find this nerve in Ameirus catus and

Macrones nemurus respectively. Sagemehl (1885) homologized the characinid claustrum with the first neurapophysis (i.e., neural arch) and the scaphium with the second neurapophysis (fide Kindred, 1919). It is generally agreed that the number of neural arches is the same as the number of spinal ganglia, (Balinsky, 1961). Because of the occurrance of the small additional spinal nerve, with its ganglion anterior to the first vertebra and its processes, but posterior to the claustrum, and because of the dorsal position of the claustrum, the claustrum must be an intercalated neural arch of a lost vertebra. It could also belong to a vertebra fused with the basioccipital. Supporting evidence for this hypothesis exists in the observation that in the channel catfish the number of segmented muscles in the anterior region is in accord with the number of spinal nerves plus their ganglia and with the number of neural arches if, and only if, the claustrum is counted as a neural arch. It is probably homologous with the intercalated arch described in the haddock, Gadus aeglifinus (Faruqi, 1935).

Scaphium: (Tables I and II)

Most investigators believe that the scaphium represents a modified neural arch of the first vertebra. Matveiev (1929), Watson (1939), and Niazi (1963) discovered that the scaphium has two origins: the basidorsal of the first vertebra contributes to the ascending and articulating processes and the independent mesenchymal cells contribute to the horizontal process (Table II).

In the channel catfish the ascending and the condylar processes are homologous to the basidorsal of the first vertebra. The horizontal process, developed from the ossification of independent mesenchymal

cells and connected with the basidorsal of the first vertebra, is homologous with the epineural dorsal rib of the first vertebra.

Intercalarium: (Tables I and II)

Most of the comparative anatomists regarded the intercalarium as a modified neural arch of the second vertebra. Sorensen (1895) went farther and considered it as a neural arch of the second vertebra plus an ossified ligament or ossified ligament only. Embryological studies by Matveiev (1929), Watson (1939), Butler (1960) and Niazi (1963), showed that the intercalarium has a double origin. The neural arch of the second vertebra forms the ascending and articulating processes while the ossified mesenchymal cells give rise to the horizontal process (Table II).

It is easy to homologize this ossicle in the cyprinids since the intercalarium in this group articulates with the second vertebra. In most cases the intercalarium in this group consists of three processes: the articular, ascending and horizontal processes.

In most adult siluroids the intercalarium is a small ossicle embedded in the interossicular ligament and has no connection with any vertebra. The morphology of this ossicle in Amiurus catus led Wright (1885) to conclude that he could not determine its homology because of its reduced condition. Bridge and Haddon (1893) discovered that in some siluroids such as Macrones, Liocassis, and Pseudobagrus the intercalarium is similar to that of cyprinid fishes. It articulates with the second vertebra and it is situated between the second and third spinal nerves. Bridge and Haddon (1893) stated that the morphology of the intercalarium in the three genera mentioned above brings the Siluridae into conformity

with the Cyprinidae. They considered these genera primitive with respect to their intercalaria. Wright (1884) considered the whole Weberian apparatus in siluroids a specialization over that of the cyprinids. Watson (1939) supported by Martin (1963) believed that the Weberian apparatus in "Cyprinoids" has been derived from that of the Siluroids. Watson based his conclusion on his observation of the intercalarium in the family Siluridae. He stated that the basidorsal of the second vertebra in the family Siluridae does not contribute to the formation of the intercalarium and he believed that the adult condition in the catfishes corresponds to the embryonic condition in the goldfish and therefore he considered the catfishes primitive.

The intercalarium in the adult channel catfish is small, irregularly cylindrical, embedded in the interossicular ligament, and has no connection to any vertebra. It is difficult to homologize it by examining the adult only. The developmental stages of the channel catfish proved that the basidorsal of the second vertebra (at least in the larva) does participate in the formation of the intercalarium. During the development of the larva, the horizontal process appears. This process joins the basidorsal of the second vertebra from its proximal side and is embedded in the interossicular ligament from the distal side. The only difference between this ossicle in the channel catfish larva and that of the cyprinid adults is that it is immovable in the channel catfish larva and movable in the cyprinid fishes. The horizontal process which includes both the shaft and the manubrium incudis in the larva is homologous to the epineural dorsal rib of the second vertebra. With development the cartilaginous basidorsal of the second

vertebra degenerates and, as far as I can see, is replaced by membrane bone which fuses into the neural arch of the complex vertebra. As the larva grows and the Weberian ossicles start functioning, the function of the epineural dorsal rib of the second vertebra also changes. As a result the proximal portion of the horizontal process (i.e., the shaft) atrophies and only the distal portion (i.e., the manubrium incudis) remains embedded in the interossicular ligament. These findings support the statement of Bloom and Fawcett (1962) that bone is a plastic tissue and the disuse of a bone is followed by atrophy and a loss of its substance.

The morphology of the intercalarium in the adult cyprinid then corresponds to the larval condition in the channel catfish and, therefore, cyrpinids must be considered less specialized and not vice versa. This conclusion supports Wright (1884) and Bridge and Haddon (1893) and rejects Watson's (1939) and Martin's (1963) hypothesis.

Tripus: (Tables I and II)

There is no agreement among comparative anatomists concerning the homology of this ossicle. Nusbaum (1881) and Kindred (1919) considered the tripus as a modified rib of the third vertebra. Grassi (1883) and Karandikar and Masurikar (1954) believed that it is a transverse process of the third vertebra. Baudelot (1868) and Bridge and Haddon (1893) considered the tripus either a rib or a transverse process of the third vertebra. Chranilov (1927) believed that the tripus originated from the parapophysis plus the rib of the third vertebra. Hora (1922) and Tilak (1964) are the only two who believed that the tripus originated from the transverse process as well as from the ribs of the third and fourth

vertebrae. Sorensen (1895) stated that the tripus originated from the rib of the third vertebra plus ossification of the interossicular ligament and swim bladder (Table I).

Different workers in the field of embryology had different conclusions concerning the origin and homology of the parts of the tripus (Table II).

In the channel catfish the tripus consists of three processes: the anterior process, the articular process, and the crescentic process. The anterior process has two origins; the inner margin originates from the epipleural rib of the third vertebra; the remains of the anterior process originate from the ossified interossicular ligament. The articular process and most of the proximal portion of the crescentic process originate from the basiventral of the third vertebra after its replacement with the membranous bone. The distal portion of the crescentic process develops from the direct ossification of the tunica externa of the swim bladder. These results are more in agreement with those of Niazi (1963), who worked on a cyprinid fish, than with those of Wright (1884) who worked on an ictalurid fish.

In conclusion, the disagreement between the workers concerning the homology of the Weberian ossicles may be attributable to differences in study material, the different interpretations, and finally, as Branson (1962) implied, there is no reason to suspect that embryological development of a cypriniform, for example, should be exactly like that of the siluriform.

The development of the first four vertebrae of the channel catfish was studied initially in newly-hatched larvae 8 mm in total

length. The notochord at this stage is represented by large, centrally-vacuolated cells, surrounded by the peripheral notochordal cells. According to Ramanujam (1929), MacBride (1932), Faruqi (1935) and Mookerjee, et al. (1940) the peripheral notochordal cells secrete the elastica externa. In this stage the sclerotomic cells migrate and aggregate around the elastica externa forming the perichordal sheath primordium. The notochord in this stage, with its elastica externa, is uniform in diameter showing no dilations in the elastica externa or localized thickenings in the perichordal sheath primordium. The peripheral notochordal cells become thickened in regions opposite the middle of the myotomes and separate from the elastica externa. This separation leaves spaces, eventually occupied by the elastica interna. Coincidental with the thickening of the peripheral notochordal cells, thickenings also occur in the mesenchymal cells of the perichordal sheath in the future intervertebral regions. In this stage the segmented notochord is not of uniform diameter. As the larva grows, the intervertebral spaces increase in size and are occupied by the elastica interna secreted by the thickened peripheral notochordal cells (Mookerjee, et al., 1940). As the intervertebral spaces increase in size, the elastica externa overlying the spaces thins and the perichordal sheath ossifies except in the future intervertebral regions. In this stage, before the structural degeneration of the elastica externa in the intervertebral regions, the swim bladder grows dorsally, bounding the notochord in the region of the future second, third and the fourth vertebrae. It is possible that the growth of the swim bladder induces the perichordal sheath in the intervertebral region, anterior to the third and fourth vertebrae, to ossify with the rest of

the perichordal sheath. As a result of the ossification there are no longer demarcations between either the second and third, or the third and fourth vertebrae. This process results in the formation of the complex centrum. The complex centrum in Siluriformes is composed of three fused vertebrae, while in Cyrpiniformes it is composed of two fused vertebrae (Greenwood, et al., 1966).

In 9.5 mm larvae the first pair of basidorsals and the basiventrals of the third and fourth vertebrae are in the condensed mesenchymal stage, while the second, third and fourth are in the procartilaginous stage. The distal portion of the third and fourth basidorsals in this stage are below the dorsal surface of the spinal cord. These two basidorsals are completed dorsally by aggregated mesenchymal cells. In 12.7 mm larva all of the basidorsals and basiventrals mentioned in the last stage have become cartilaginous. Although Ramanujam (1929), Faruqi (1935) and Mookerjee, et al.(1940) stated that the neural arches do not rest directly on the notochordal sheath, my observations show that they do rest on, and, in fact, fuse with the elastica externa of the notochord, with the exception of the first pair of basidorsals which contribute to the scaphia, and consequently contribute to the formation of the centrum of the complex vertebra. In addition to the basidorsals in this stage, there are independent aggregations of mesenchymal cells between the basidorsals and between the first pair of basidorsals and the exoccipitals. The distal portions of the third and fourth basidorsals of one side are widened and fused dorsally with those of the other side. As development proceeds the cartilaginous neural spines of the third and fourth vertebrae will form, and the dorsolateral

sides of the third and fourth basidorsals will fuse on each side. In a larve of 20.0 mm the connective tissue surrounding the cartilaginous neural spines ossifies and the first four basidorsals are replaced by bone proceeding dorsoventrally. Coincidental with this, the mesenchymal cells between the second and third basidorsals and the third and fourth basidorsals ossify. These ossifications together with the cartilaginous bone of the third and fourth basidorsals form the complex neural arch, within which the oval slits are located. The mesenchymal cells between the second basidorsals and the exoccipitals form connective tissue in which the claustra and scaphia are located.

CHAPTER IV

SWIM BLADDER

The Morphology of the Swim Bladder in the Adult

The swim bladder in the adult channel catfish is of the physostomous type. It is cordate in shape with its wide, anterior end located underneath and attached to the complex vertebra and its processes. Its rounded, narrow, posterior end is free and extends posteriorly beyond the level of the most posterior extension of the parapophysis of the fourth vertebra.

Ventrally, the swim bladder is separated from the abdominal viscera by the dorsal peritoneum, which reflects laterally and lines the body wall below the level of the swim bladder, forming a retroperitoneal dorsal cavity. In this retroperitoneal cavity the swim bladder is surrounded by loose connective tissue and fat.

Internally, the swim bladder has two septa dividing the internal cavity into three chambers (TS and LS, Plate XVI, Fig. 3). The transverse septum is located just ventral to the fourth vertebra and is wider and thicker ventrally than dorsally. A longitudinal septum, perpendicular to the transverse septum, divides the posterior two-thirds of the swim bladder cavity into two parallel right and left chambers. Two interchamber apertures are located between the lateral edges of the incomplete

transverse septum and the lateral walls of the swim bladder (ICA, Plate XVI, Figs. 3 and 5). A direct communication between each posterior chamber and the anterior chamber exists through the interchamber apertures.

The anterior chamber has two anterolateral protuberances; the head kidney lies in the shallow depression separating them. The tunica externa of the anterolateral protuberances is attached to the post temporal plates and to the anterior part of the fourth parapophysis. A slightly more defined depression in the middorsal side of the anterior chamber is occupied by and firmly attached to the ventral and lateral sides of the centrum of the complex vertebra (CC, Plate XVI, Fig. 3). Extending posteriorly along the middorsal side of the longitudinal septum, the groove vanishes before the posterior end of the swim bladder. The crescentic processes of the tripodes and the radial nodules, with the radial fibers between them, are embedded in the tunica externa of the dorsal side of the anterior chamber (TR.C, RN and RF, Plate XVI, Fig. 3).

The thin lateral sides of the anterior chamber are attached on either side of the body wall at areas devoid of muscular tissue. These areas have been called "the lateral cutaneous areas," (Bridge and Haddon, 1893), and can be seen from the outside in preserved specimens (LCA, Plate XVI, Fig. 1). They may be considered analogous to the tympanic membrane of higher vertebrates in receiving vibrations.

The two parallel posterior chambers are free, being unattached to either the vertebral column or the body. The kidneys are located above and posterior to the two posterior chambers.

Histologically, the wall of the swim bladder in the adult consists of the tunica externa and the tunica interna. The tunica externa consists of two strata of white, tough, fibrous connective tissue. Each stratum is composed of many fibers parallel to each other. The parallel fibers of one stratum obliquely cross the parallel fibers of the other stratum.

The tunica interna is a thin, transparent layer that lines the entire wall of the swim bladder and is easily separated from the thick, tough tunica externa. It consists of two thin sheets fused together--a simple squamous epithelial sheet on the inside, covered by a very thin connective tissue sheet. These two sheets are not easily distinguishable from each other and in some cases from the tunica externa without a knowledge of their developmental history.

Anterior to the stomach the long, narrow pneumatic duct joins the dorsolateral right side of the esophagus to the midventral side of the anterior chamber immediately anterior to the transverse septum. Most of the pneumatic duct lies between the two sheets of the dorsal mesentery. However its distal portion enters the retroperitoneal cavity before opening into the swim bladder.

Histologically, the portion of the pneumatic duct near the esophagus has the same general layers as that of the esophagus. Since the muscularis mucosa which normally separates the lamina propria from the submocosa is absent, in both the esophagus and the proximal portion of the pneumatic duct, these two layers are continuous.

The outer layer of the tunica muscularis consists of circular striated muscles while the inner layer is composed of longitudinal

striated muscles. Although the layer of circular muscles is well developed and defined, the longitudinal muscle fibers are sparsely scattered throughout the region of the original submucosa.

The distal portion of the pneumatic duct has no observable tunica muscularis; only the connective tissue layer of the submucosa plus the lamina propria remain outside. The simple cuboidal epithelium remains inside. The two layers are surrounded by the dorsal mesentery except where they enter into the retroperitoneal cavity of the swim bladder.

Histologically the wall of the distal portion of the pneumatic duct is the same as the tunica interna of the swim bladder.

The Development of the Swim Bladder

8.3 mm larva, 110 hr after fertilization (Plate XVII, Figs. 2-4)

There is little if any definite indication of either the swim bladder or the pneumatic duct before 80 hr. At 110 hr, however, there are unmistakeable indications of both the swim bladder and the pneumatic duct. By 127 hr the form of these is constant and definite.

The swim bladder diverticulum develops as an evagination from the right dorsolateral wall of the foregut (SB.D, Fig. 2). This evagination proceeds posteriorly, paralleling the dorsolateral right side of the gut and pushing ahead of it the splanchnic mesoderm which surrounds the foregut. The diverticulum, near its junction with the foregut, is embedded within the splanchnic mesoderm surrounding the foregut endoderm (Figs. 2 and 3). This portion of the diverticulum will serve as the origin of the pneumatic duct. The distal portion of the diverticulum

lies within the dorsal mesentery and will develop into the swim bladder (SB.P, Figs. 3 and 4). The distal portion in this stage is still below the level of the dorsal peritoneum (DP, Figs. 3 and 4). In this stage at any level, a cross section of the diverticulum has almost the same shape and diameter as the dorsal aorta (DA, Fig. 3).

The walls of the swim bladder diverticulum are formed from two tissue layers, an inner layer of simple cuboidal epithelial cells of endodermal origin and an outer thick layer of undifferentiated splanchnic mesoderm. The outer splanchnic mesodermal layer, which is continuous with that of the foregut outer layer and essentially indistinguishable from it, forms the mesodermal portion of the tunica interna of the swim bladder.

10.4 mm larva, 152 hr after fertilization (Plate XVII, Figs. 6-8)

As development proceeds, the swim bladder diverticulum elongates, growing posterolaterally, paralleling the dorsal, right side of the foregut and lying within the dorsal mesentery.

At 152 hr the swim bladder increases in length and diameter, forming an oblong vesicle growing posteriorly and middorsally above the level of the dorsal peritoneum (SB, Figs. 5 through 8). It is bounded dorsally by the dorsal aorta, dorsolaterally by the pronephric ducts, anteriorly by the anterior portion of the kidneys, posterodorsally by the posterior portion of the kidneys and ventrally by the dorsal peritoneum (Figs. 5 through 8).

Both the swim bladder and the pneumatic duct are lined with simple cuboidal epithelium, except at their anterior juncture where columnar epithelium appears.

11.1 mm larva, 170 hr after fertilization (Plate XVIII, Figs. 2-4)

Important changes in the development of the swim bladder and the pneumatic duct occurred by this stage:

(1) The dimensions of the swim bladder and its lumen, which is probably filled with fluid, have increased slightly since the preceding stage (Figs. 1, 2, and 3).

(2) The pneumatic duct now opens anteroventrally into the midventral side of the anterior end of the swim bladder (PD, Figs. 1 and 2).

(3) There is migration and aggregation of somatic mesodermal cells peripheral to the swim bladder. These aggregated mesenchymal cells condense, forming a complete mesodermal layer around the swim bladder. These cells are the origin of the tunica externa of the swim bladder [SOM(TE) Fig. 2]. Between this condensed somatic mesodermal sheath and the primitive swim bladder, loose somatic mesodermal cells, are clearly seen between the lateral sides of the primitive swim bladder and the outer condensed somatic mesodermal sheath. Because of the location of these cells, I shall refer to them as the "inter-tunic layer" (IT, Fig. 3).

At the apex of the posteromidventral portion of the condensed somatic mesodermal sheath, a longitudinal thickening of somatic mesoderm appears (LS.P, Figs. 3 and 4). This longitudinal ridge grows anterodorsally toward the entrance of the pneumatic duct, pushing the ventral splanchnic mesodermal layer of the swim bladder before it. This growth results in a coalescence, first of the midventral portion of the endodermal epithelial layer with that of the middorsal portion of the

same layer (Fig. 3), and secondly of the two splanchnic mesodermal layers (Fig. 4).

The next stage will show the coalescence of the longitudinal ridge from the midventral side with the middorsal side of the condensed, somatic, mesodermal layer. Thus the two posterior chambers are formed.

11.5 mm larva, 182 hr after fertilization (Plate XVIII, Figs. 6-8).

As the larva develops, the amount of yolk decreases while the mass of the swim bladder and the other visceral organs increases.

In this stage the pneumatic duct elongates posterolaterally, while the swim bladder increases in all dimensions. The continued posterior growth of the pneumatic duct pushing against the attached growing swim bladder, produces a posteriorly directed loop in the distal portion of the pneumatic duct, terminating immediately before the latter enters the midventral side of the anterior portion of the swim bladder (PD, Fig. 5).

With the increase in dimensions and the dorsal growth of the swim bladder, the dorsoventral diameter of the dorsal aorta along the entire anterodorsal half of the growing swim bladder is reduced (DA, Fig. 6). This may be caused by the pressure of the dorsal growth of the swim bladder.

The epithelial cells of the swim bladder, formerly cuboidal, now are flattened. These are not of uniform height, but are tallest near the pneumatic duct, grading to squamous cells at the most distal part of the swim bladder (Figs. 5, 6, and 7). In those areas where the epithelium becomes thin there is some indication of separation of this layer of epithelium from the surrounding splanchnic mesoderm (Figs. 5, 6, and 7).

Coincident with this separation, the intervening space is filled with a foamy matrix, probably secreted by the endodermal epithelial layer lining the swim bladder.

The partitioning of the swim bladder begun earlier, continues anteriorly toward the opening of the pneumatic duct. Posterior from this opening the midventral portion of the intertunic layer fuses with that of the middorsal portion of the same layer. At the posterior end, the growing longitudinal ridge of somatic mesodermal cells meets and fuses with the middorsal condensed somatic mesoderm (LS, Fig. 8) with a resultant division of the original posterior chamber of the swim bladder, posterior to the opening of the pneumatic duct, into two compartments. Each compartment has similar complements of endodermal epithelial tissue surrounded by a splanchnic mesoderm surrounded in turn, by the loose connective tissue (the intertunic), with the tunica externa (a condensed somatic mesodermal layer) forming the final outermost layer. Part of the somatic mesoderm of the tunica externa forms the median portion of the longitudinal and the transverse septa of the swim bladder.

12.3 mm larva, 200 hr after fertilization (Plate XIX, Figs. 2-6)

A number of changes have occurred between the last stage and this one:

(1) The posteriorly directed loop of the pneumatic duct is more pronounced (Fig. 1).

(2) The anterior and lateral growth rate of the anterior chamber has been faster than has the posterior and lateral growth of the two posterior chambers (Figs. 1, 3, and 4).

(3) The longitudinal septum is completed; it is short and thick (LS, Fig. 3).

(4) The transverse septum, which will partially separate the anterior chamber from the two posterior ones in the adult, has just started to develop. This growth starts at the ventral portion of the anterior end of the longitudinal septum, posterior to the opening of the pneumatic duct, and grows dorsolaterally (TS.P, Fig. 4).

(5) The complete separation of the epithelial lining from the splanchnic mesoderm and the filling of the intervening space with the foamy matrix has occurred (Figs. 1 through 4).

(6) The foamy matrix is invaded by capillary networks and cells. The cells appear to migrate from the endodermal epithelium lining the swim bladder. These cells perhaps use the foamy matrix as a substrate upon which to migrate.

(7) The splanchnic mesoderm in this stage forms a layer one cell in thickness except in the areas near and around the junction of the pneumatic duct with the swim bladder (SPM, Figs. 2, 3, and 4). The cells of this layer are closely attached to each other.

(8) The "intertunic" connective tissue cells still persist in this stage and are between the splanchnic mesoderm and the outer condensed somatic mesoderm (IT, Figs. 2, 3, and 4).

(9) The bifurcation of the anterior chamber into the antero-lateral protuberences has just started.

13.0 mm larva, 224 hr after fertilization (Plate XX, Figs. 4-6)

In this stage, although the swim bladder increases in width and length both anteriorly and posteriorly, the growth anteriorly is still

more rapid (Fig. 2). The swim bladder extends from the level of about the middle of the second vertebra to the end of the fifth (Fig. 3). Its anterior chamber is about the same length as its two posterior chambers. The transverse septum separating the anterior from the two posterior chambers is located below the level of the fourth basiventrals (TS, Figs. 3 and 5). The anterior chamber not only increases in length, but also in width, while its lateral walls become thinner than the other walls (Fig. 4).

The foamy matrix layer increases in thickness while the endodermal epithelial layer decreases in gradients proceeding anteriorly and posteriorly from the opening of the pneumatic duct into the swim bladder (Figs. 1 and 2).

The endodermal epithelial layer becomes convoluted as the lumen of the swim bladder decreases. At the same time the overall distance between the splanchnic mesoderm, the loose connective tissue cells of the intertunic layer and the condensed somatic mesoderm decreases (IT, Fig. 6).

The thick, short, longitudinal septum, completely formed in the last stage, is elongated and thin. It has differentiated into tough, white connective tissue. The transverse septum which started to develop in the last stage is completely formed now; it is thick and wide, incompletely separating the anterior chamber from the two posterior ones (TS, Fig. 5).

In this stage the pneumatic duct continues to extend posterolaterally, paralleling the right dorsal wall of the foregut and the midgut (Figs. 1, 5, and 6). The juncture of the pneumatic duct with the

esophagus becomes visible at the level of the first vertebra in this stage. The duct reaches the level of the fifth basiventrals (Figs. 1, 2, and 6), and turns dorsoanteriorly, opening into the midventral side of the anterior chamber of the swim bladder at the level of the fourth basiventrals (Figs. 2 and 5).

Stages between 14.0 mm larva, 263 hr after fertilization and 17.0 mm larva, 457 hr after fertilization (Plate XXI, Figs. 1-6)

In 14.0 mm larva the foamy matrix increases in mass; the lining epithelium of the swim bladder is further convoluted, and the lumen of the swim bladder greatly reduced. The splanchnic mesoderm is located much closer to the tunica externa. This process results in a further condensation of the intertunic connective tissue layer (Fig. 1).

In a 14.6 mm larva the large accumulation of foamy matrix starts to disappear. The lining epithelium fuses with the splanchnic mesoderm and forms the tunica interna of the swim bladder (Fig. 2). The swim bladder lumen and the intertunic area increase in size (Fig. 2).

In 15.5 mm larva the foamy matrix has completely disappeared. The fused epithelial layer and the splanchnic mesodermal layer (i.e., tunica interna) are still separated from the tunica externa by the very loose connective tissue of the intertunic layer (IT, Fig. 3).

The two strata of the tunica externa, the outer longitudinal oblique and the inner circular oblique, can be seen in this stage for the first time.

In 17.5 mm larva the tunica interna is adherent to the inner wall of the tunica externa and the intertunic area is reduced. The

development of the swim bladder in this stage is completed and represents the condition of the swim bladder in the adult fish (Figs. 4, 5, and 6).

Discussion

The swim bladder in the adult channel catfish

The swim bladder in the adult channel catfish is flat, cordate in shape and of the physostomous type. The flattened shape according to the theory of ellipsoidal balloons must be maintained by internal ties or by pressure of the surrounding viscera (Alexander, 1966). Since the latter is not true in the channel catfish, the shape of the swim bladder must be maintained by the internal partitions. As was noticed by Dobbin (1941) there are two internal septa. A longitudinal septum divides the posterior portion of the swim bladder, posterior to the opening of the pneumatic duct, into two parallel right and left chambers; and an incomplete medial transverse septum perpendicular to the longitudinal septum at its anterior end. This septum does not reach the lateral walls of the bladder, so that there is an aperture between each posterior chamber and the anterior one. There is no direct communication between the two posterior chambers, i.e., communication between the two posterior chambers is possible only through the anterior (Weberian) chamber.

The origin of the swim bladder

There are two embryological patterns of formation of the swim bladder in teoleosts, (1) as an evagination from the endoderm of the foregut, and (2) as a solid mass of mesoderm later invaded by an endodermal diverticulum from the foregut.

In the first case, there are three places at which the endodermal evagination has been noted to take place: (a) from dorsal side of the foregut as in Catostomus commersoni (Nelson, 1959), and Opsanus tau (Tracy, 1911); (b) from the right side of the dorsal wall of the foregut as in Lepomis macrochirus (Duwe, 1952), Hemichromis bimaculata (McEwen, 1940), and Fundulus heteroclitus (Tracy, 1911); and (c) from the left side of the dorsal wall of the gut, just anterior to the liver duct diverticulum as in Micropterus salmoides (Johnston, 1953), and Stolephorus mitchilli (Tracy, 1911).

In the second case the solid mass of mesodermal cells, more probably splanchnic mesoderm, appears first between the endodermal epithelium of the foregut and the two sheets of peritoneum of the dorsal mesentery. This mass is located on the right side of the dorsal wall of the foregut. An endodermal diverticulum at that level begins to grow into the mass, as in Salmo salar (Hoar, 1937).

The distal portion of the diverticulum in both patterns expands to form the swim bladder, while the proximal portion forms the pneumatic duct. In the channel catfish the swim bladder diverticulum arises first as an evagination from the right side of the dorsal wall of the foregut. This endodermal evagination pushes in front of it the splanchnic mesoderm surrounding the foregut at that site, proceeding in its growth posterolaterally through the dorsal mesentery.

The diverticulum in a larva of 110 hr (8.3 mm) is still within the dorsal mesentery, below the dorsal peritoneum. The distal portion of the diverticulum in this stage has no noticeable lumen and has the same diameter as that of the proximal portion.

In a larva of 128 hr (9.5 mm) the distal portion of the diverticulum is growing into the region bounded dorsally by the dorsal aorta and dorsolaterally by the pronephric ducts. Upon leaving the dorsal mesentery the distal portion of the diverticulum, possibly because no longer confined, begins to expand simultaneously with the formation of a lumen.

It is possible that there is a two-way induction between the distal portion of the swim bladder diverticulum and the somatic mesenchymal cells peripheral to it. This induction causes both to differentiate. The distal portion of the diverticulum together with its lumen dilates, while the peripheral somatic mesenchymal cells aggregate, condense, and finally form the tunica externa of the swim bladder. This kind of two-way induction has been observed in tissue cultures of developing metanephric tubules (fide Ebert, 1965). The swollen portion of the distal part of the swim bladder diverticulum is the primitive swim bladder (Nelson, 1959), while the proximal rapidly elongating portion of the diverticulum is the beginning of the pneumatic duct.

The primitive swim bladder in this stage is similar to that of the adult salmon described by Tracy (1911). With respect to the swim bladder, the channel catfish would appear, then, to show a greater degree of specialization than the salmon.

The development of the chambers

In teleosts the embryonic pneumatic duct opens either into the anterior or into the posterior end of the primitive swim bladder. According to Tracy (1911), the primitive type of swim bladder is that

which has a pneumatic duct communicating with its anterior end; the derived type being that which has the embryonic pneumatic duct communicating with its posterior end. This generalization is not true in Fundulus heteroclitus, Menidia menidia and Esox (Tracy, 1911).

In both physostomous and physoclistous teleosts there are species having swim bladders composed of two or even three chambers (Jones and Marshall, 1953). The origin of the anterior chamber in physostomous fishes such as Stolenphorus mitchilli (Tracy, 1911) and Catostomus commersoni (Nelson, 1959) is from the expansion of the anterior wall of the primitive swim bladder. After the formation of the anterior chamber the primitive swim bladder is usually named the posterior chamber or the primitive portion, while the anterior chamber is usually named the secondary portion or the Weberian chamber in Ostariophysi.

In physoclistous fishes such as the toadfish (Opsanus tau), the pipefish (Siphostoma fuscum), the cunner (Tautogolabrus adsprsus) and the tautog (Tautoga onitis), the embryonic pneumatic duct opens into the posterior end of the primitive swim bladder, its distal portion contributing to the formation of the posterior chamber after the proximal portion of the pneumatic duct atrophies (Tracy, 1911).

In a 128-hr (9.5 mm) channel catfish larva, only the swollen distal portion of the endodermal diverticulum has a noticeable lumen. There are two places where the mesodermal cells are more condensed, those anterior to the primitive swim bladder and those posteroventral to it. In later stages, these condensed cells prove to be of somatic mesodermal origin.

During development, the primitive swim bladder increases in length and in other dimensions, while the pneumatic duct increases in length and slightly in diameter. The portion of the swim bladder near the entrance of the pneumatic duct grows posteriorly less than the pneumatic duct itself. The U-shaped curvature of the pneumatic duct is thus caused by the rapid growth of the primitive pneumatic duct between its origin and its entrance into the swim bladder. The degree of curvature of this loop in the pneumatic duct continues to increase during the development of the swim bladder.

Coincidental with the growth of the pneumatic duct and its gradual curvature, the three chambers of the swim bladder develop.

In a 186-hr (12 mm) channel catfish larva, the anterior face of the primitive swim bladder dorsal to the entrance of the pneumatic duct near the condensed mesodermal cells, expands, but especially anterolaterally. This expansion may be brought about by means of the condensed mesodermal cells in that area. This expansion is the beginning of the anterior chamber of the swim bladder. Concomitant with the development of the anterior chamber, the pneumatic duct is no longer joinging the swim bladder from its anterior end, but from its mid-ventral side.

Coincidental with the formation of the primitive swim bladder, there is aggregation and condensation of somatic mesodermal tissue, peripheral to and possibly induced by the primitive swim bladder. This condensed somatic mesodermal tissue is the origin of the tunica externa (Tracy, 1911; Jones and Marshall, 1953). Between the condensed somatic

mesodermal tissue and the primitive swim bladder is a layer of loose somatic mesodermal cells named "intertunic layer."

The condensed somatic mesodermal tissue thickens on the posteromidventral side of the primitive swim bladder, grows anterodorsally and brings about the fusion of the growing ventral ridge with the middorsal portion of the condensed somatic mesoderm and the developing longitudinal septum.

The condensed ventral somatic mesoderm forms a thickened ridge which appears to push the intertunic layer, the splanchnic mesodermal layer and the epithelial layer up into the lumen of the swim bladder. This process progresses anteriorly and dorsally until the ridge fuses with the middorsal wall of the swim bladder. The epithelial, splanchnic mesodermal and the intertunic layers, separate after fusion forming with the somatic mesodermal layer the longitudinal septum. The anterior extension of the longitudinal septum divides and shifts laterally at the junction of the pneumatic duct to form two laterally growing wings or septa. These septa never fuse with the lateral walls of the swim bladder. The aperture remaining is the interchamber aperture. Each chamber has the following from inside to outside: (1) epithelial, (2) splanchnic mesodermal, (3) intertunic, and (4) the condensed somatic mesodermal (tunica externa) layers. The first two layers form the tunica interna.

The initial inflation of the swim bladder

Four theories concerning the origin of the initial gas in the swim bladder have been proposed:

(1) The gulping in or air at the surface of the water. This theory was propounded by Vogt (1842) and supported by Ledebur (1928), Ledebur and Wunder (1937), and Jacobs (1937). Johnston (1953) observed that the larvae of Micropterus salmoides never rise to the surface of the water to gulp in air during the early stages of swim bladder inflation, but still have inflated swim bladders. McEwen (1940) and Niazi (1963) prevented the larvae of Hemichromis bimaculata and Pimephales promelas, respectively, from gulping air. In spite of this, their swim bladders were well inflated. Clemens and Sneed (1957) reported that the larvae of the channel catfish come to the surface initially at about nine days after fertilization (about 216 hr). In collections made in 1964, I observed that the larvae came to the surface at about 227 hr. The serial sections indicate an inflated swim bladder occurs for the first time at about 336 hours, at least 100 hr elapses between the time a young larva comes to the surface and the time its swim bladder is initially inflated. These observations along with the following experiment demonstrate rather conclusively that gulping air at the surface is not required for initial inflation of the swim bladder of the channel catfish.

The experiment was conducted at the University of Oklahoma Biological Station, Lake Texoma, during the summer of 1965. Fertilized eggs of channel catfish were placed in a small screen-wire box. The box with the eggs inside was placed in circulating water near the bottom of a tall aquarium and kept for about ten days. The water was circulated in such a way as to avoid trapping air bubbles in the water of the aquarium.

Upon examination of serial sections of these larvae, I found that the swim bladders were inflated; they were identical to those of larvae, in another aquarium, allowed to reach the surface.

(2) Cellular breakdown. According to this theory Powers (1932), hypothesized that there are certain organic materials in the epithelial cells, lining the swim bladder which break down producing CO_2 in the swim bladder lumen. McEwen (1940) and Johnston (1953) supported this theory. I would suggest that a qualitative analysis of the initial gas in the swim bladder by gas chromatography would strongly support or deny this hypothesis.

(3) Digestive processes. Johnston (1953) believed that some of the initial gas may come from the digestive processes, since the pneumatic duct remains open during the early inflation of the swim bladder.

(4) Complex capillary network. Proposed by Koch (1934), the theory states that the capillary network in the swim bladder secretes the initial gases into the swim bladder (fide Johnston, 1953). Johnston rejected this theory simply because he found no capillary network in the swim bladder of Micropterus salmoides. McEwen (1940) did not find a capillary network in Hemichromis bimaculata. There does, however, appear to be a very transient capillary network between the endodermal columnar epithelial layer and the splanchnic mesodermal layer of the swim bladder in the channel catfish. This network first appears in the 186-hr larvae and reaches its peak of development by 200 hr, declining and disappearing shortly thereafter. I feel that the network contributes to the formation of the swim bladder lumen by secreting very small amounts

of gas into a very spongy, gel-like material I choose to call the "foamy matrix."

The first indication of the formation of the foamy matrix appears in larvae of 182 hr, (11.5 mm). In this stage a few scattered cavities appear near the capillaries. These cavities are filled with fluid. When these cavities are formed, the endodermal columnar cells begin to flatten and at the same time the foamy matrix appears. I agree with Niazi (1963) that this material is a product of the epithelial cuboidal cells lining the swim bladder, rather than with Nelson (1959) who stated that it is the product of mesoderm surrounding the epithelium. Lymph escaping between the lining endothelial cells of the capillaries may also contribute to this material since the capillaries also appear for a short period only.

Nelson (1959) referred to the transient matrix in Catostomus commersoni as "transient intertunic matrix" and Niazi (1963) referred to the matrix in Pimephales promelas as "intraepithelial matrix." I do not agree with either of them on this nomenclature, because their photomicrographs show that this foamy matrix occupies the same place as the matrix of the channel catfish. Because it is located between the epithelial lining of the swim bladder and the splanchnic mesoderm, and since the tunica interna is formed from the epithelial layer and the splanchnic mesoderm, I would suggest naming it the "intratunica interna matrix." The isolated masses of the matrix increase gradually and finally join to form a continuous layer of material looking like a foam, since there are many vacuoles in it.

During the formation of the continuous layer of intratunica interna matrix, endodermal cells grow, divide, and soon move into that foamy matrix, appearing to use it as a substratum for their movement. This unusual conclusion, that these endodermal cells are moving into the foamy matrix, is supported by the following observations: in 183-hr (11.5 mm) larvae, the cells composing the endodermal epithelium appear to have begun active mitosis with a consequent accumulation of cells along the surface of the epithelium adjacent to the foamy matrix. In just later larvae, these cells have either been pushed by the accumulation of new cells under them or have migrated, from the endodermal epithelium and appear in the foamy matrix near the endodermal epithelium. At still later larval stages, these cells appear still farther into the matrix. By 200-hr (12.3 mm) larvae the endodermal cells have become dispersed over the entire region of the foamy matrix. This observation is similar to the situation observed by Patten, et al. (1948) in the case of the endothelial cells invading the cardiac jelly in the heart of the chick embryo and the formation of a tissue, resembling the mucous connective tissue in transition to the definitive structure of the heart.

As the development proceeds, the mass of the foamy matrix, as well as the number of capillaries increase. The capillaries reach their maximum development in a larva of 200 hr (12.3 mm); soon after, they become reduced and finally disappear. The foamy matrix reaches its maximum volume in larvae of 263 hr (14.0 mm). In this stage the lumen of the swim bladder in obliterated, and the intertunic connective tissue cells are condensed. By 283 hr (14.2 mm), the foamy matrix begins to disappear,

possibly because of the coalescences of the small vacuoles and the consequent formation of the lumen of the swim bladder. Part of the foamy matrix with the few cells in it remains between the epithelial layer and the splanchnic mesoderm, forming the tunica interna of the swim bladder. The complete disappearance of the foamy matrix has occurred by the 336 hr (15.6 mm) larval stage and the tunica interna is completely formed. The lumen of the swim bladder has increased in dimensions and the intertunic cells of the swim bladder have become loose aggregates.

My observations support Koch's (1934) theory since I found capillaries in the intratunica interna matrix. I believe that the capillaries and the intratunica interna matrix are concerned with the initial inflation of the swim bladder in the channel catfish.

Finally, the initial inflation of the swim bladder in teleosts is probably more complex than we now hypothesize and probably varies among the different groups, perhaps even within the same group of fishes. Morphological study of serial sections alone may not completely solve the problem. The only real solutions are through the routes of experimental embryology, tissue culture, and the analysis of both the foamy matrix and the gases in the newly-formed swim bladder.

CHAPTER V

SUMMARY

(1) The Weberian apparatus in the adult channel catfish, as in other Ostariophysi, consists of two functional units, the pars sustentaculum and the pars auditum.

(2) The pars sustentaculum is composed of the nonmoveable parts of the first vertebra and the complex vertebra.

(3) In the adult, the complex vertebra appears to be a single structure, i.e., no intervertebral ligaments or swollen areas can be observed between its separate components.

(4) The complex vertebra is composed of three fused vertebrae.

(5) The neural arch of the complex vertebra is formed from the bony basidorsals of the second, third, and fourth vertebrae and from the ossified connective tissue between them.

(6) Although the first and second vertebrae lack neural spines, the third and fourth neural spines are long and interconnected by a vertical ridge.

(7) The anterior and posterior portions of the fourth parapophysis originate from the basiventrals of the fourth vertebra and its pleural ribs with ossification of the connective tissue between the basiventrals and pleural ribs and the neural arch of the complex vertebra.

(8) The pars auditum consists of paired units of ossicles, one unit lying on each side of the pars sustentaculum. In the channel catfish, each unit is composed of four ossicles; anteriorly to posteriorly they are, the claustrum, scaphium, intercalarium, and tripus. The functionally moving chain, linking the swim bladder to the auditory ossicles, appears to be composed of the scaphium, the intercalarium, and the tripus, exclusive of the claustrum.

(9) The posterior, thick, cartilaginous portion of the claustrum is homologized with the basidorsal of a lost vertebra; the anterior, thin portion arises directly from ossified mesenchymal cells.

(10) The three processes of the scaphium originate in the following way:

(a) The anterior horizontal process, develops from direct ossification of mesenchymal cells located anterior to the basidorsals of the first vertebra, and is homologous to the epineural rib of the first vertebra.

(b) The ascending and condylar processes originate from the basidorsal of the first vertebra.

(11) The intercalarium in the adult channel catfish is small, and is embedded in the interossicular ligament, with no connection to any vertebra. It is homologous with the tip of the epineural rib of the second vertebra.

(12) The tripus is the largest ossicle in the series. Its three processes originate in the following way:

(a) The anterior process is homologous with the epipleural rib of the third vertebra plus ossification in the ligamentum tripus.

(b) The articular process and most of the crescentic process originate from the basiventral of the third vertebra. The distal portion of the crescentic process originates from the direct ossification of the tunica externa of the swim bladder.

(13) The dorsal lamina and the radial nodule are homologous with the epipleural rib of the fourth vertebra.

(14) The swim bladder arises as an evagination from the right side of the dorsal wall of the foregut. In the adult, it has two septa dividing the internal cavity into three chambers, an anterior chamber and two parallel posterior chambers. There is no communication between the two posterior chambers except through the anterior chamber.

(15) The longitudinal septum starts its development as an anterodorsal growth from the posteromidventral side of the outer wall of the swim bladder.

(16) After the completion of the formation of the longitudinal septum, the incomplete transverse septum arises immediately posterior to the opening of the pneumatic duct, growing in a ventrodorsal direction.

(17) A capillary network appears between the endodermal epithelial and the splanchnic mesodermal layers of the swim bladder by the 182-hr larval stage. This network is embedded in a foamy matrix, the intratunica interna matrix.

(18) Experimental evidence indicates that the initial inflation of the swim bladder does not result from gulping air at the surface by the young larva. The capillary network in the intratunica interna matrix seems to play a significant part in this inflation process. The role appears to be the secretion of the initial gases into the swim bladder lumen.

(19) The capillary network is very transient, since it reaches maximal development by 200 hr and begins to decline, disappearing shortly thereafter. The intratunica interna matrix, on the other hand, while reaching peak enlargement by 263 hr, does not disappear until about the 336-hr larval stage.

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A P P E N D I X

TABLE I

SUMMARY OF COMPARATIVE MORPHOLOGICAL STUDIES CONCERNING THE HOMOLOGY OF THE WEBERIAN OSSICLES

	Claustrum	Scaphium	Intercalarium	Tripus
(1) Baudelot (1868)	Neural spine, or divided intercrural bone of V_1	Neural arch of V_1	Neural arch of V_2	Transverse process or rib of V_3.
(2) Nusbaum (1881)	Neural spine of V_1	" " " "	" " " "	Rib of V_3
(3) Grassi (1883)	Part of the skull	" " " "	" " " "	Transverse process of V_3.
(4) Sorensen (1890)	Neural spine of V_1	" " " "	" " " "	" "
(5) Chranilov (1927)	Neural process of V_1	" " " "	" " " "	Parapophysis plus rib of V_3.
(6) Karandikar and Masurikar (1954)	Neural spine of V_1	" " " "	" " " "	Transverse process of V_3
(7) Kindred (1919)	Intercalated cartilage	" " " "	" " " "	Rib of V_3
(8) Sorensen (1895)	Interspinous ossicle	" " " "	" " " " plus ossified ligament or ossified ligament only	" " " plus ossified ligament plus ossified swim bladder.

TABLE I--(Continued)

	Claustrum	Scaphium	Intercalarium	Tripus
(9) Bridge and Haddon (1893)	Neural spine of V_1	Neural arch of V_1	Neural arch of V_2	Transverse process or rib of V_3
(10) Mookerjee, et al. (1954)	Absent	Neural arch of V_1	Neural arch of V_2 (It is so small that they considered it absent.)	Second and third rib and ossified fibrous tissue
(11) Hora (1922)	A part of neural arch of V_1	A part of neural arch of V_1	A part or whole of the neural arch of V_2	Transverse process and rib of V_3 plus rib of V_4
(12) Sagemehl (1885)	First true neurapophysis (neural arch)	Second neurapophysis (neural arch)	?	?
(13) Tilak (1964)	A part of neural arch of V_1	A part of neural Arch of V_1	Neural arch of V_2	Transverse process and rib of V_3 plus rib of V_4

1, 2, 3, and 4 -- After Bridge and Haddon, 1893.
5 and 8 -- After Martin, 1963.
7 -- After Branson, 1962.
12 -- After Kindred, 1919.

TABLE II

SUMMARY OF EMBRYOLOGICAL STUDIES CONCERNING THE HOMOLOGY OF THE WEBERIAN OSSICLES

	Claustrum	Scaphium	Intercalarium	Tripus
(1) Wright (1884)	Spinous process of V_1	Neural arch of V_1	Modified neural arch of V_2	The anterior part from transverse process of V_3. The posterior part (crescentic process) from ossification in the tunica externa of the air bladder.
(2) Matveiev (1929)	Spinal process of first vertebra	Neural arch of V_1 and mesenchyme	Neural arch of V_2 and mesenchyme	Rib of V_3 (?) and mesenchyme
(3) Watson (1939)	Crescentic accumulation of mesenchyme cells that become directly ossified (intercalated structure)	Ascending and articulating processes from basidorsal of V_1. Concha stapedis (horizontal process) from independent mesenchyme.	Manubrium incudis from ossification in interossicular ligament. Ascending and articulating processes from basidorsal of V_2.	Anterior process from basiventral of V_3 plus ossification in interossicular ligament. Articulating process from basiventral of V_3. Main body from mass of mesenchyme between third and fourth basiventrals. Transformator process from rib rudiment

TABLE II--(Continued)

	Claustrum	Scaphium	Intercalarium	Tripus
(4) Butler (1960)	Ossification of mesenchyme	Basidorsal of V_1	Articular + ascendening process from basidorsal of V_2. Manubrium incudis from small island of bone in the interossicular ligament.	Anterior tip of anterior ramus from interossicular ligament. Body and most of anterior ramus from basidorsal of V_3. Transformator process and part of posterior ramus from dorsal rib of V_3.
(5) Niazi (1963)	Ossification of mesenchyme	Ascending and articulating processes from basidorsal of V_1. Concha stapedis from a membranous bony rod embedded in mesenchyme.	Articular + ascending process from basidorsal of V_2. Manubrium incudis from small island of bone in the intercssicular ligament.	Anterior and posterior rami from interossicular ligament. Body from interossicular ligament, mesenchyme and part of the third basiventral. Articulating process from the third basiventral. Transformator process from direct ossification in the tunica externa of the swim bladder.

2 - After Branson, 1962.

THE MORPHOLOGY OF THE WEBERIAN APPARATUS IN THE ADULT

(Abbreviations)

AIL - Articular facet for the interossicular ligament
ALS - Articular facet for the ligamentum scaphium
AOG - Aortic groove
APSB - Anterior projection of the superficial bone
ARF - Articular facet for the radial fibers
$ARTP_4$ - Articular facet for the anterior part of the 4th parapophysis
ASI - Atrial cavity
B - Brain
BOC - Basioccipital
BP - Basapophysis
BR - Bony ridge
CART - Cartilage
CC - Complex centrum
CDG - Canal for the cardinal vein
CL - Claustrum
COB - Concavity of the basioccipital
CSI - Cavum sinus imparis
C_1 - Centrum of the first vertebra
C_{2-3-4} - Complex centrum composed of the 2nd, 3rd, and 4th centra
C_5 - Centrum of the fifth vertebra
DE - Ductus endolymphaticus
DL - Dorsal lamina
DP - Dorsolateral pit
EP - Epiotic
EXO - Exoccipital
FM - Foramen magnum
GCL - Groove for the cleithrum
HP - Horizontal plate of the exoccipital
IL - Interossicular ligament
IN - Intercalarium
IPT - Inferior limb of the posttemporal
LR - Lateral ridge
MD - Median depression
NC - Neural canal
$NS_{3,4,5}$ - Neural spines of the 3rd, 4th, and 5th vertebrae
NTA - Anterior notch
NTP - Posterior notch
OS - Oval slit
PT - Posttemporal

PTO - Outer limb of the posttemporal
P_4A - Anterior part of the 4th parapophysis
P_4P - Posterior part of the 4th parapophysis
P_5 - 5th parapophysis
RF - Radial fibers of the tripodes
RN - Radial nodule
RSC.H - Recess for the horizontal process of scaphium
SB - Superficial bone
SC - Scaphium
SC.A - Ascending process of the scaphium
SC.C - Condylar process of the scaphium
SC.H - Horizontal process of the scaphium
SE - Sinus endolymphaticus
SI - Sinus imparis
SOC - Supraoccipital
SOCS - Supraoccipital spine
TR - Tripus
TR.A - Anterior process of the tripus
TR.ART - Articular process of the tripus
TR.C - Crescentic process of the tripus
VARP - Ventral articulating process of the first vertebra
VRN - Vertical ridge connecting the 3rd and 4th neural spines

Plate I

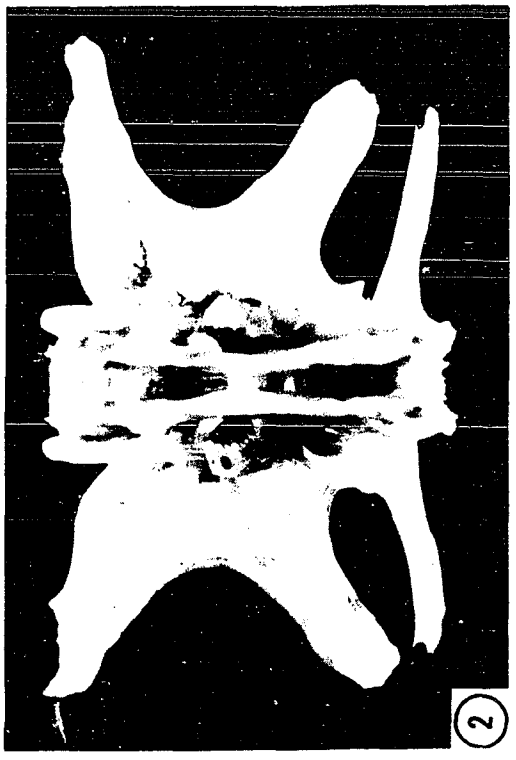
Fig. 1 - Dorsal view of the pars sustentaculum including the fifth vertebra and the tripodes (pleural of tripus), 1.4 X.

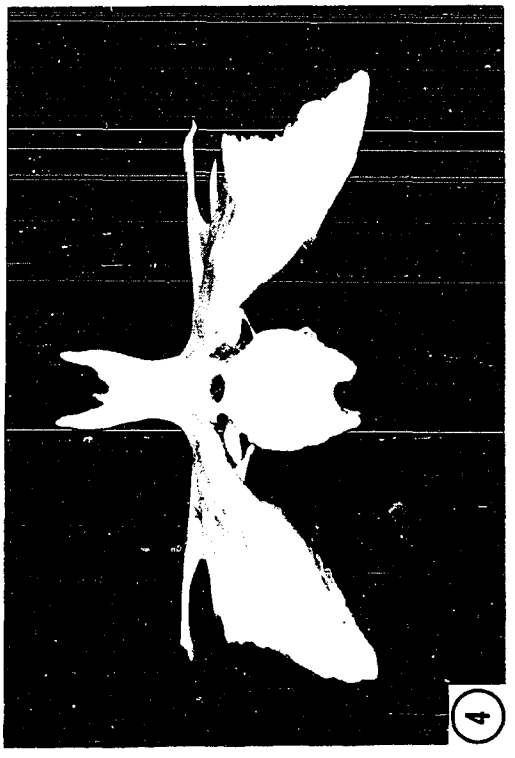
Fig. 2 - Ventral view of the pars sustentaculum including the fifth vertebra and the tripodes, 1.4 X.

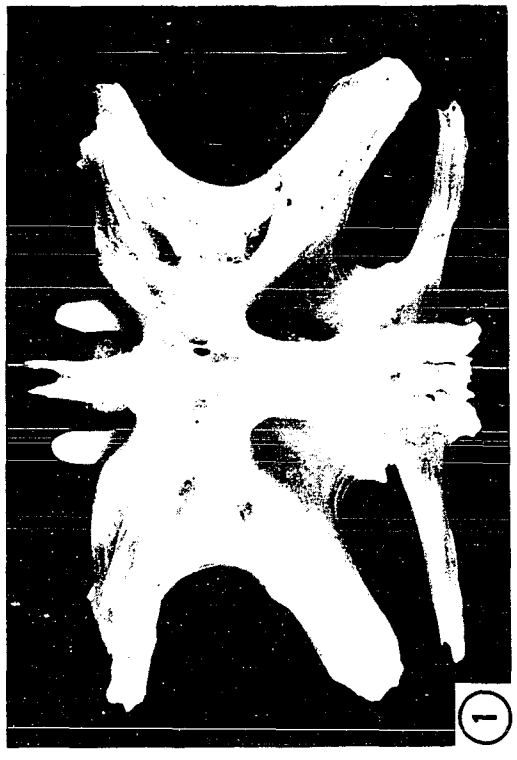
Fig. 3 - Lateral view of the pars sustentaculum including the fifth vertebra and the tripodes, 1.4 X.

Fig. 4 - Anterior view of the pars sustentaculum including the fifth vertebra and the tripodes, 1.4 X.

Plate I







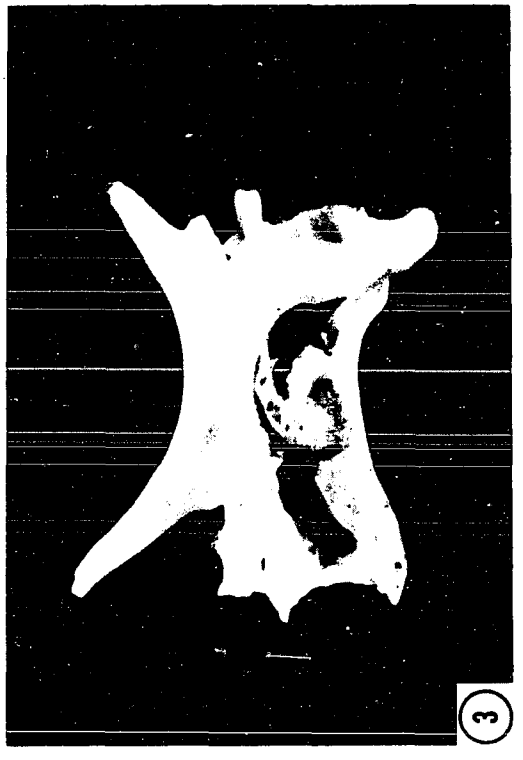
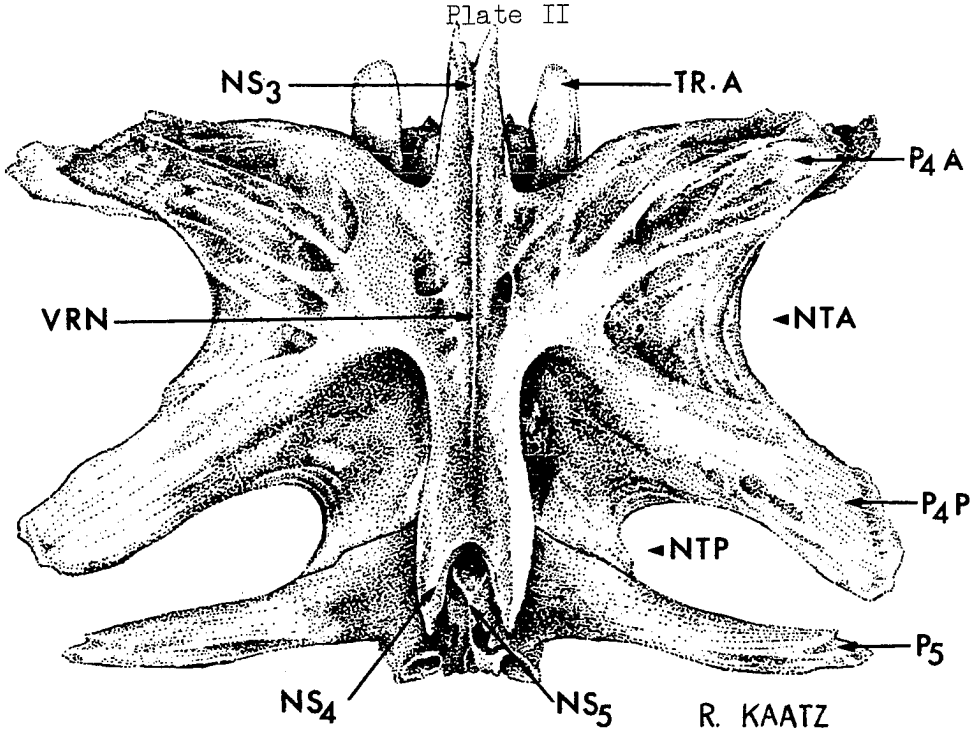


Plate II

Fig. 1 - Dorsal view of the pars sustentaculum including the fifth vertebra and the tripodes, 1.9 X.

Fig. 2 - Ventral view of the pars sustentaculum including the fifth vertebra and the tripodes, 1.9 X.

Plate II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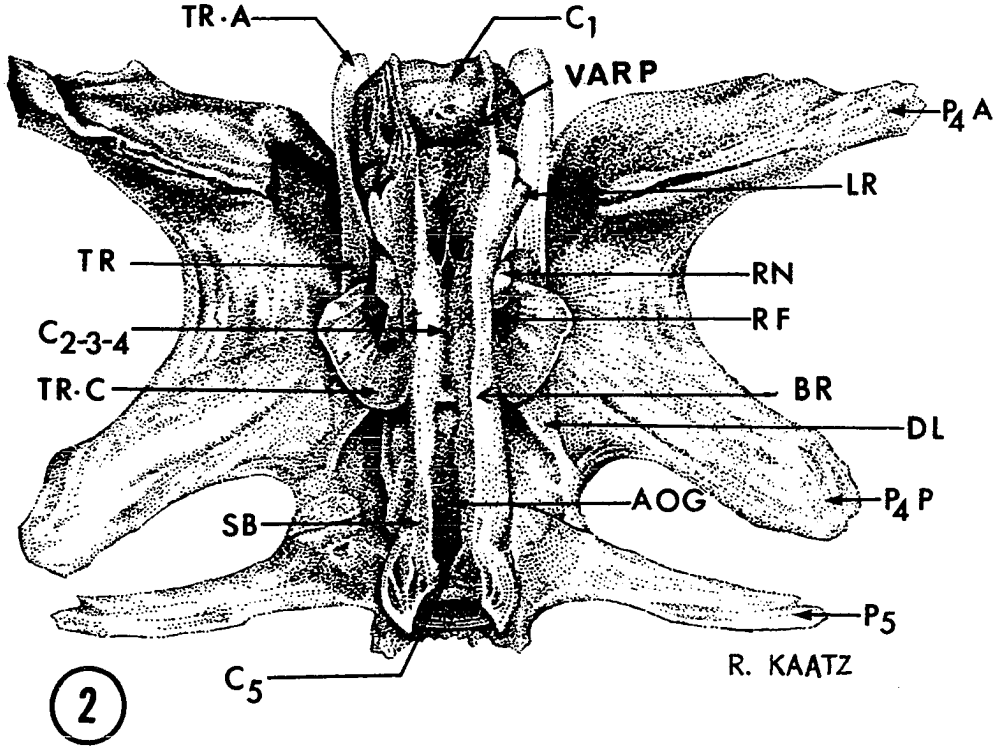
P4 A
VRN
NTA
P4 P
NTP
P5
NS4
NS5
R. KAATZ

1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C1
VARP
P4 A
LR
TR
RN
RF
C2-3-4
TR·C
BR
DL
AOG
P4 P
SB
P5
C5
R. KAATZ

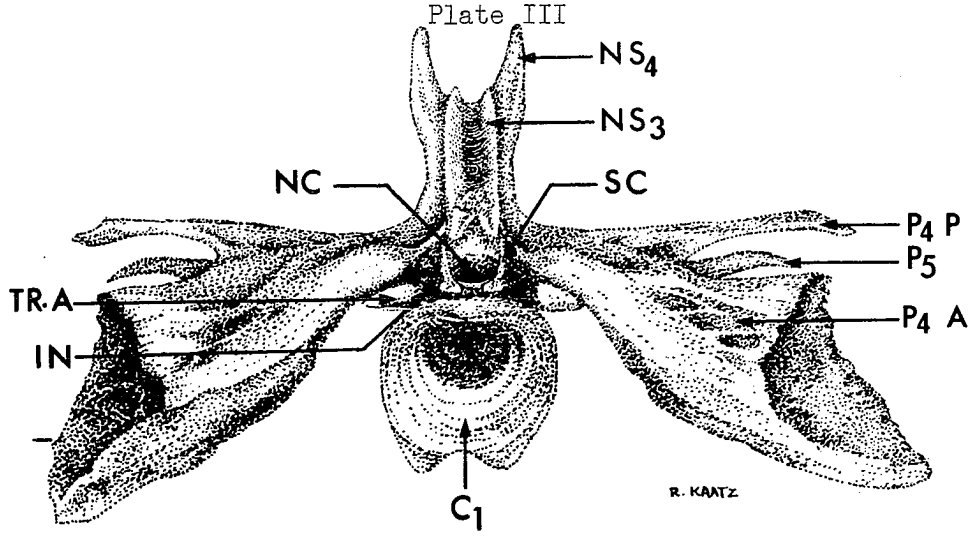
2

Plate III

Fig. 1 - Anterior view of the Weberian apparatus and the fifth vertebra. Note the fifth parapophysis, 2 X.

Fig. 2 - Lateral view of the Weberian apparatus and the fifth vertebra, 2 X.

Plate III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SC
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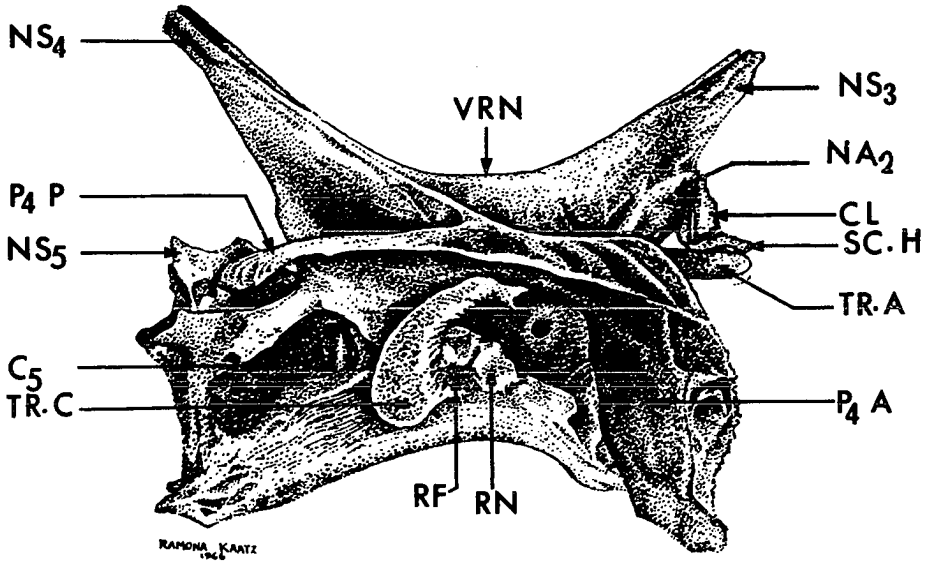
P5
TR·A
P4 A
IN
C1
R. KAATZ

1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P4 P
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NS5
SC·H
TR·A
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TR·C
P4 A
RF
RN
RAMONA KAATZ

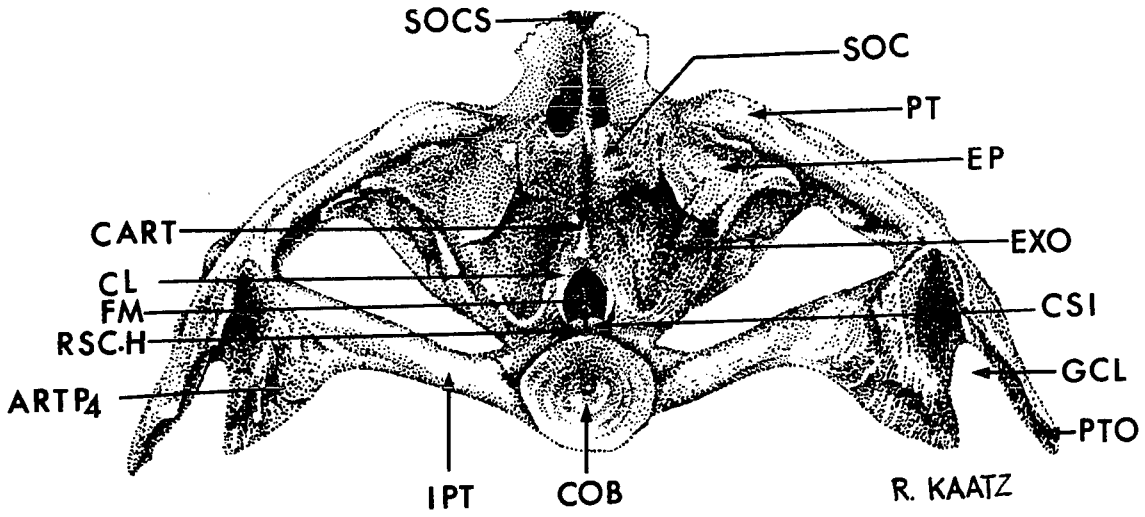
2

Plate IV

Fig. 1 - Posterior view of the occipital region, 1.7 X.

Fig. 2 - Lateral view of the pars sustentaculum including the fifth vertebra. Note that the fourth parapophysis was cut away to show the oval slit, 2 X.

Plate IV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GCL
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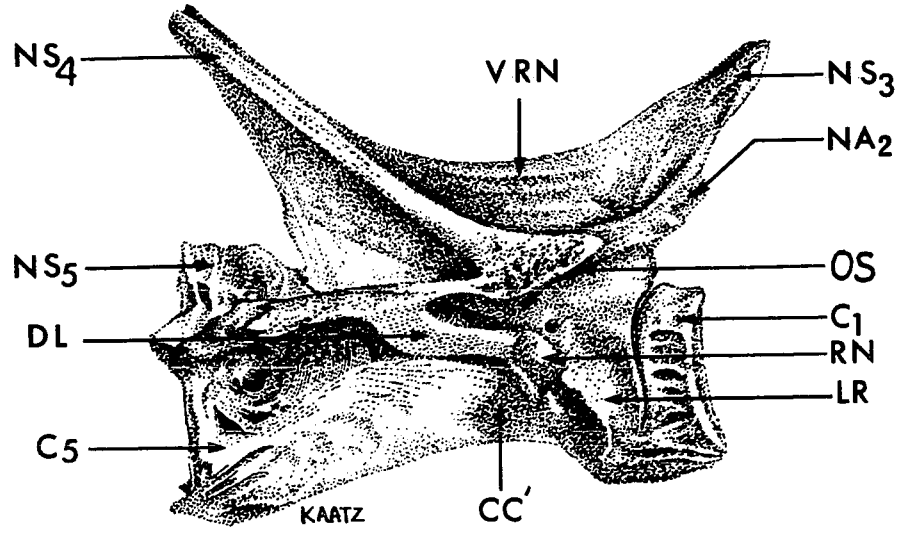
PTO
IPT
COB
R. KAATZ

1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NA2
NS5
OS
C1
DL
RN
LR
C5
KAATZ
CC'

2

Plate V

Fig. 1 - Lateral view of the first centrum. Note the scaphium and the claustrum, 2 X.

Fig. 2 - Ventral view of the first centrum, 2 X.

Fig. 3 - Anterior view of the first centrum, 2 X.

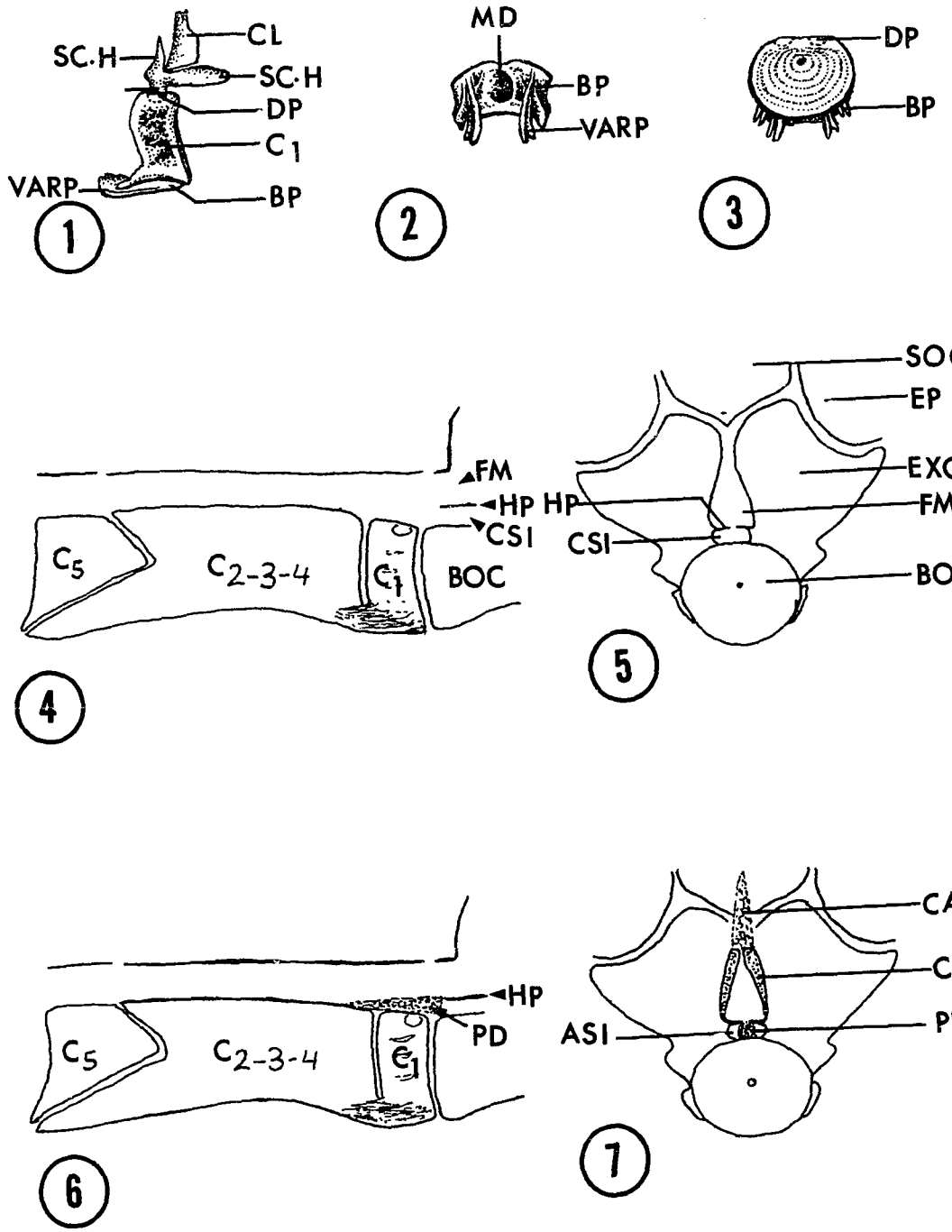
Fig. 4 - Diagrammatic lateral view of the posterior portion of the skull and the anterior centra showing the slope on the dorsal surface of the first vertebra after removal of the endorhachis, 2 X.

Fig. 5 - Posterior view of the occipital region. Note the relationships between the foramen magnum and the cavum sinus imparis, 2 X.

Fig. 6 - Diagrammatic lateral view of the posterior portion of the skull and the anterior centra showing the endorhachis, 2 X.

Fig. 7 - Posterior view of the occipital region. Note the endorhachis and the paired atrium sinus imparis, 2 X.

Plate V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BOC
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SOC
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EXO
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BOC
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PD
C5
C2-3-4
C1
6
CART
CL
ASI
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7

Plate VI

Fig. 1 - Medial view of the claustrum, 7 X.

Fig. 2 - Lateral view of the claustrum, 7 X.

Fig. 3 - Anterior view of the intercalarium, 7 X.

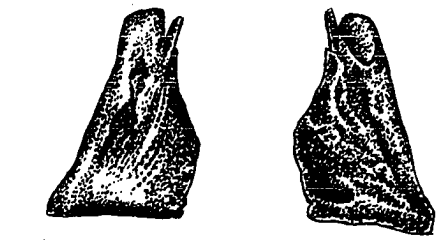
Fig. 4 - Lateral view of the intercalarium, 7 X.

Fig. 5 - Medial view of the scaphium, 7 X.

Fig. 6 - Lateral view of the scaphium, 7 X.

Fig. 7 - Diagrammatic dorsal view of the Weberian ossicles, in situ, showing the relationships of the ossicles to the posterior portion of the inner ear.

Plate VI



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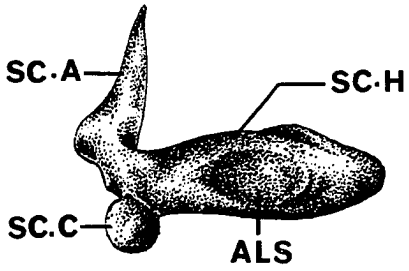

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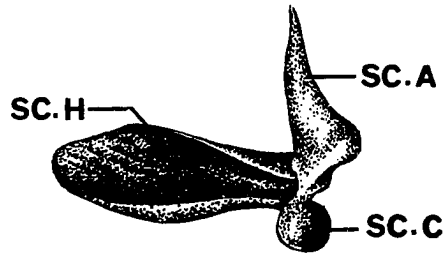

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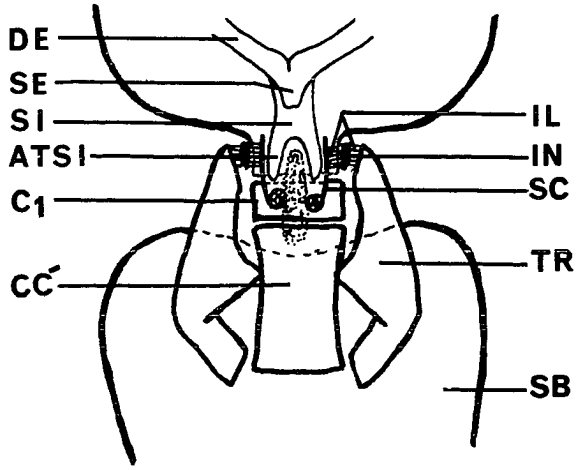


7

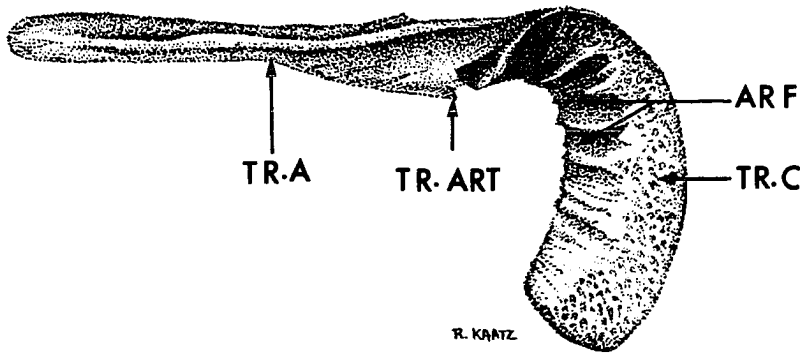
Plate VII

Fig. 1 - Lateral view of the tripus, 3.6 X.

Fig. 2 - Medial view of the tripus, 3.6 X.

Fig. 3 - Dorsal view of the tripus, 3.6 X.

Plate VII



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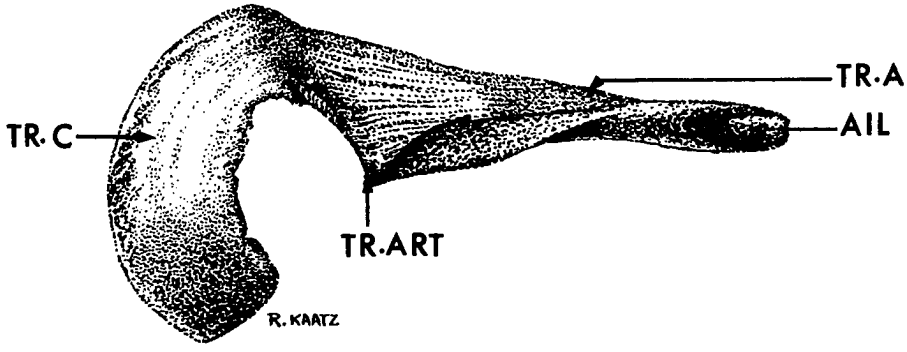

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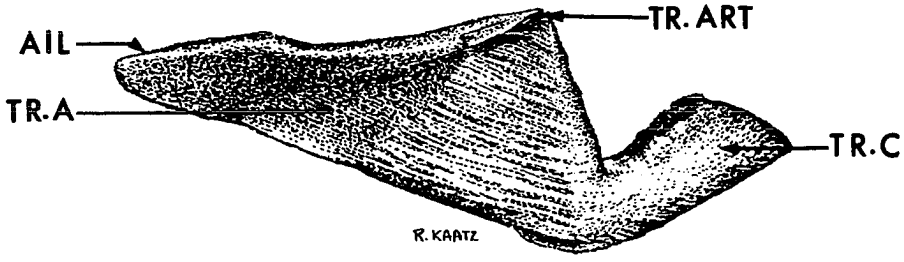


3

THE DEVELOPMENT OF THE WEBERIAN OSSICLES

(Abbreviations)

AC - Anterior chamber of the swim bladder
AMW - Anteromedial wall of the swim bladder
AS - Axial septum
ASI - Atrium sinus imparis
BD_{1-4} - Basidorsals of the first through the fourth vertebrae
BD_1(SC) - Basidorsal of the first vertebra (scaphium)
BV_{3-4} - Basiventrals of the third through the fourth vertebrae
BV_3(TR.C)- Basiventral of the 3rd vertebra (crescentic process of the tripus)
C - Centrum
C_1 - First centrum
CL - Claustrum
CLO - Ossified portion of the claustrum
DA - Dorsal aorta
DE - Ductus endolymphaticus
DL - Dorsal lamina
DLI - Dorsal ligament
EE - Elastica externa
EI - Elastica interna
ER - Endorhachis
HK - Head kidney
IBL - Interbasiventral ligament
ICS - Intracentral septum
IL - Interossicular ligament
IVR - Intervertebral ring
K - Kidney
LG - Lagena
LS - Ligamentum scaphium
LT - Ligamentum tripus
MG - Midgut
MI - Manubrium incudis
MI (IN) - Manubrium incudis (intercalarium)
MY - Myotome
NA_{3-4} - Neural arches of the 3rd and 4th vertebrae
NS_3 - Neural spine of the 3rd vertebra
NT - Notochord
NT.P - Peripheral notochordal cells
NT.V - Vacuolated notochordal cells
PCV - Postcardinal vein

PD - Pneumatic duct
P_4 - Fourth pleural rib
P_4A - Anterior part of the 4th parapophysis
PRD - Pronephric duct
PS - Perichordal sheath
PSP - Perichordal sheath primordium
RN - Radial nodule
S - Shaft of the intercalarium
SB - Swim bladder
SB.AC - Anterior chamber of the swim bladder
SBO - Superficial bone
SB.TE - Tunica externa of the swim bladder
SC - Scaphium
$SC(BD_1)$ - Scaphium (basidorsal of the first vertebra)
SC.H - Horizontal process of the scaphium
SE - Sinus endolymphaticus
SG - Spinal ganglion
SG.A - Additional spinal ganglion
SI - Sinus imparis
SN - Spinal nerve
SN_1 - First spinal nerve
SOC - Supraoccipital
SPV - Saccus paravertebralis
TE - Tunica externa
TR.A - Anterior process of the tripus
VRN - Vertical ridge connecting neural spines of the 3rd and 4th vertebra
Y - Yolk
1-5 - 1st through the 5th centra

Plate VIII

All the transverse sections are photographed as if viewed from the cephalic surface; therefore, the right side of the larva is at the reader's left.

Fig. 1 - Transverse section showing the procartilaginous basidorsals of the first future vertebra of a 152-hr, 10.4 mm-larva.

Fig. 2 - Transverse section showing the cartilaginous basidorsals of the second future vertebra, posterior to the section of Fig. 1.

Fig. 3 - Transverse section showing the procartilaginous basiventrals of the future third vertebra, posterior to the section of Fig. 2.

Fig. 4 - Transverse section showing the cartilaginous basidorsals of the third future vertebra, posterior to the section of Fig. 3.

Fig. 5 - Transverse section showing the procartilaginous basiventrals of the future fourth vertebra, posterior to the section of Fig. 4.

Fig. 6 - Transverse section showing the cartilaginous basidorsals of the future fourth vertebra, posterior to the section of Fig. 5.

Plate VIII

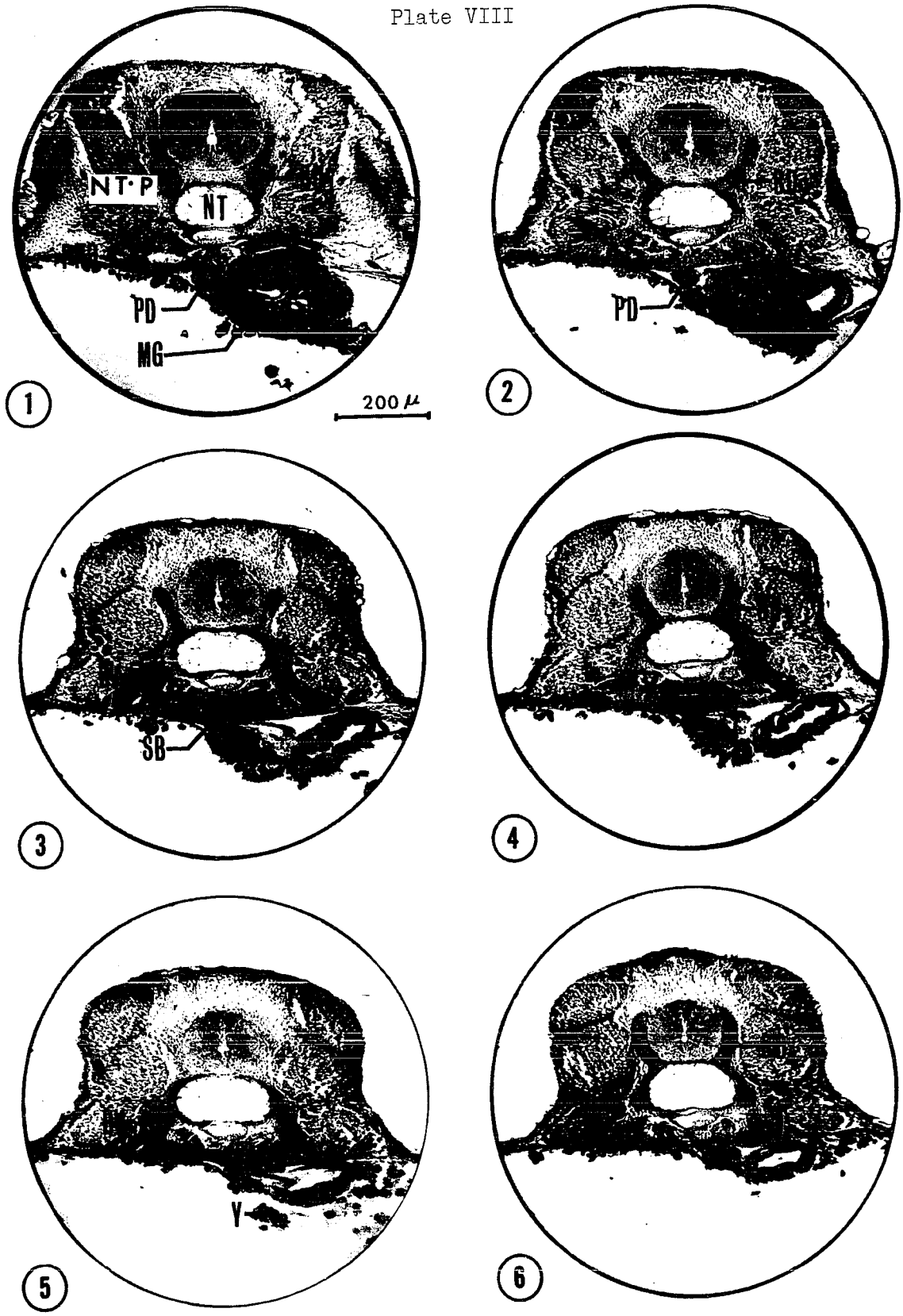


Plate IX

All the frontal sections are photographed as if viewed from the dorsal surface; therefore, the right side of the larva is at the reader's right.

Fig. 1 - Frontal section showing the first four basidorsals of a 170-hr, 11.1-mm larva. Note the aggregation of mesenchyme cells anterior to the first pair of basidorsals.

Fig. 2 - Frontal section showing the horizontal process of the scaphium and the manubrium incudis of a 194-hr, 12.1-mm larva.

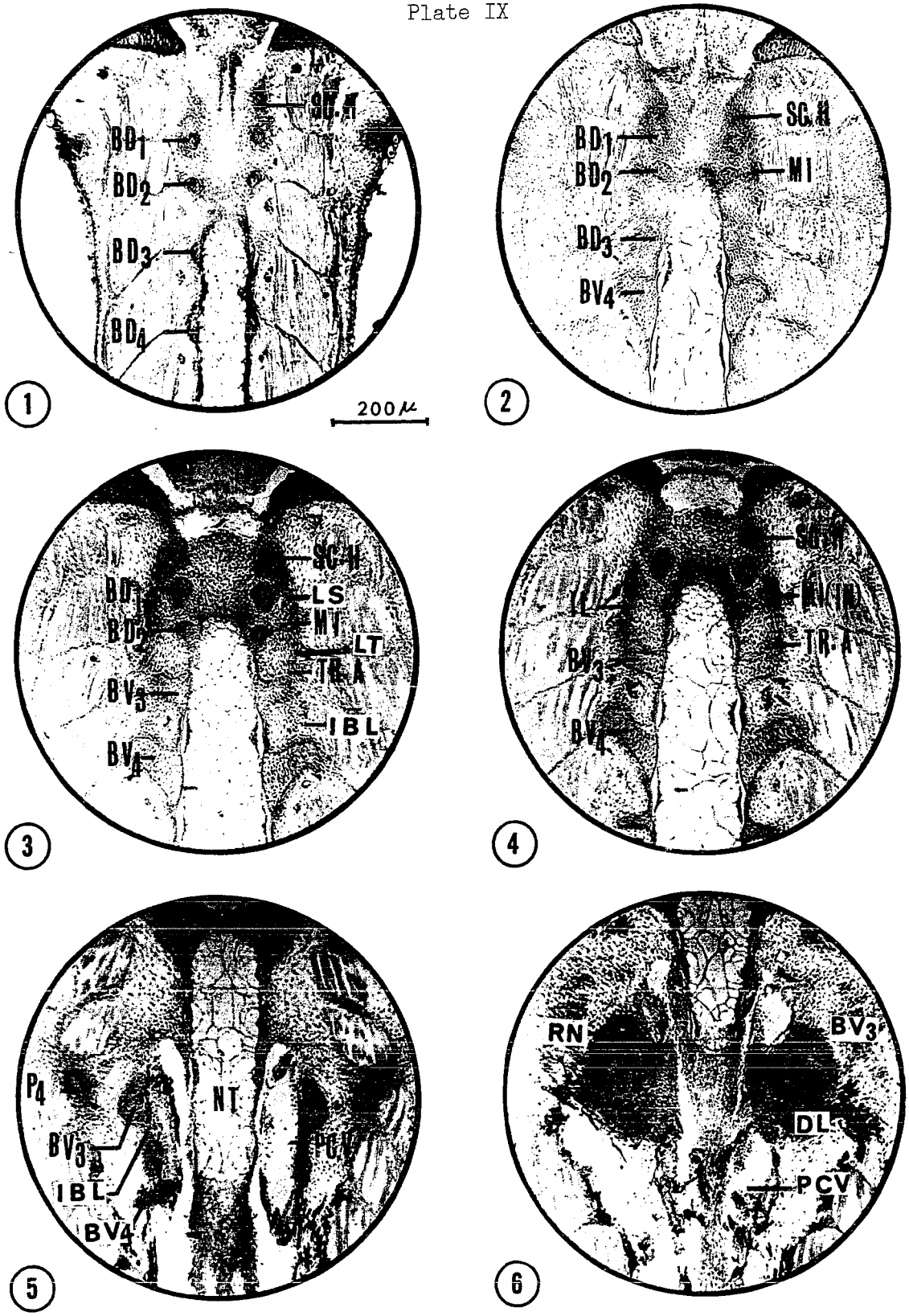
Fig. 3 - Frontal section showing the basidorsals of the first and second future vertebrae and the basiventrals of the future third and fourth vertebrae of a 200-hr, 12.3-mm larva. Note the ligamentum tripus and the anterior process of the tripus.

Fig. 4 - Frontal section, below the section of Fig. 3, showing the interossicular ligament.

Fig. 5 - Frontal section, below the section of Fig. 4, showing the basiventrals of the third and fourth future vertebrae. Note the pleural rib of the fourth vertebra and the interbasiventral ligament.

Fig. 6 - Frontal section, below the section of Fig. 5, showing the dorsal surface of the swim bladder. Note the radial nodule and the dorsal lamina.

Plate IX


SC.H
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SC.H
MT
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BV3
BV4
4
P4
BV3
IBL
BV4
NT
PCV
5
RN
BV3
DL
PCV
6

Plate X

The anterior end of all sagittal sections is at the reader's left.

Fig. 1 - Sagittal section showing the anterior first future four vertebrae of a 224-hr, 13.0-mm larva.

Fig. 2 - Sagittal section showing the basidorsals of the future first four vertebrae outward to the section of Fig. 1.

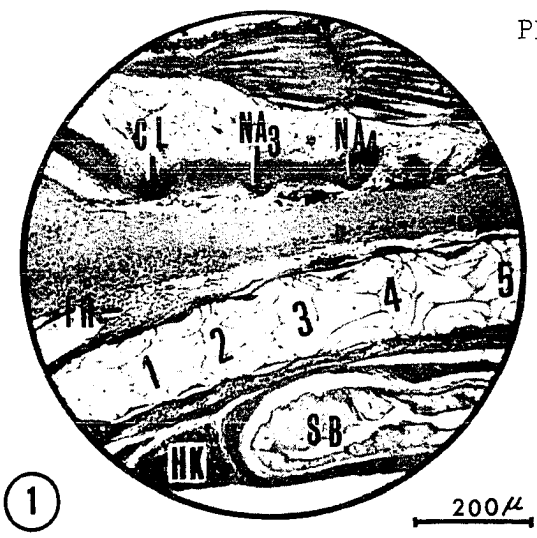
Fig. 3 - Sagittal section showing the lateral side of the notochord outward to the section of Fig. 2. Note the horizontal process and the condylar process of the scaphium.

Fig. 4 - Sagittal section showing the interossicular ligament and the horizontal process of the scaphium outward to the section of Fig. 3. Note the manubrium incudis and the basiventrals of the third and fourth future vertebrae.

Fig. 5 - Sagittal section showing the distal portions of the basiventrals of the future third and fourth vertebrae outward to the section of Fig. 4.

Fig. 6 - Sagittal section showing the pleural rib of the fourth future vertebra which will form the anterior process of the fourth parapophysis.

Plate X



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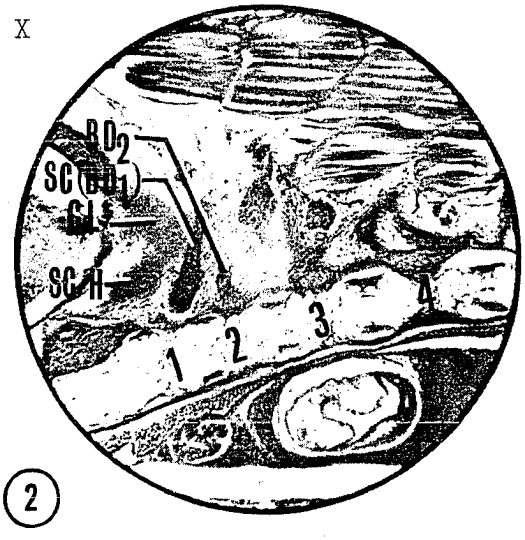
200μ



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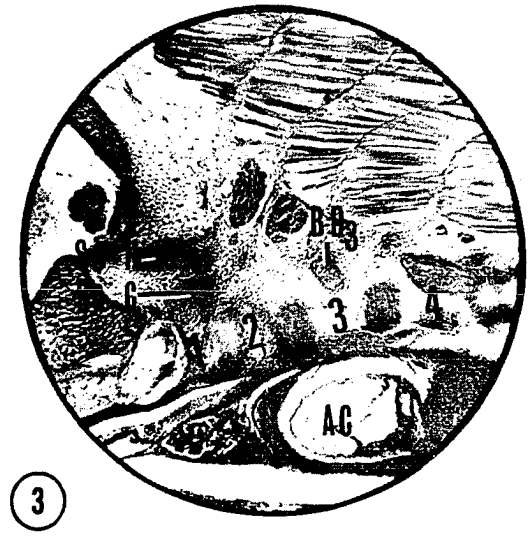

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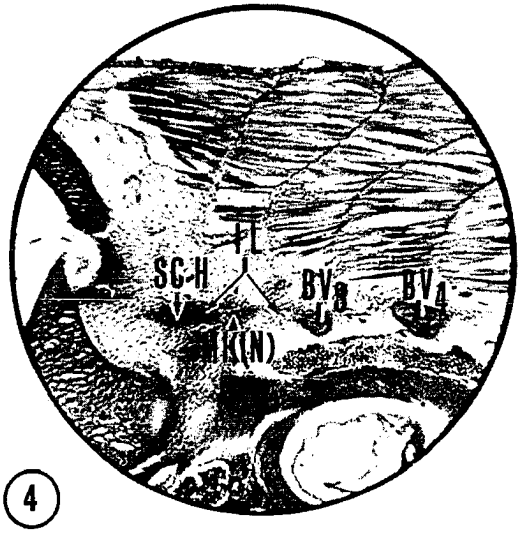

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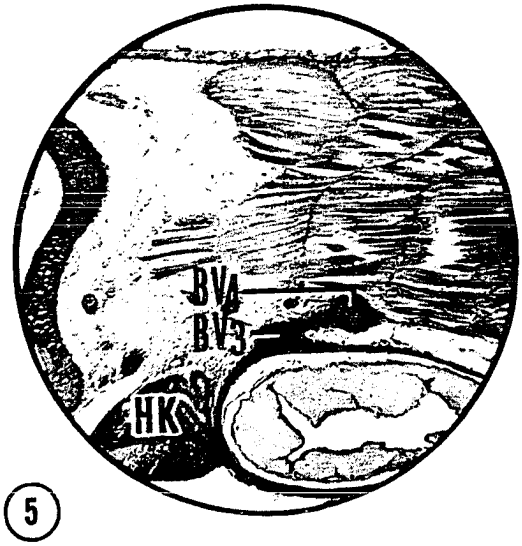

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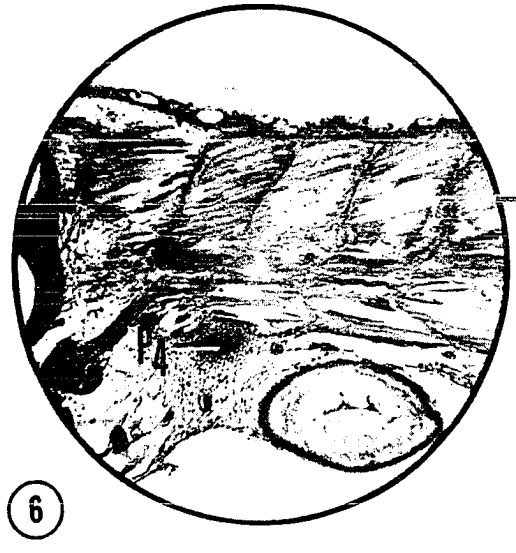


6

Plate XI

All the transverse sections are photographed as if viewed from the cephalic surface, therefore, the right side of the larva is at the reader's left.

Fig. 1 - Transverse section showing the horizontal process of the scaphium and the anterior portion of the claustrum of a 237-hr, 13.5-mm larva.

Fig. 2 - Transverse section showing the basidorsals of the first vertebra and the posterior portion of the claustrum posterior to the section of Fig. 1.

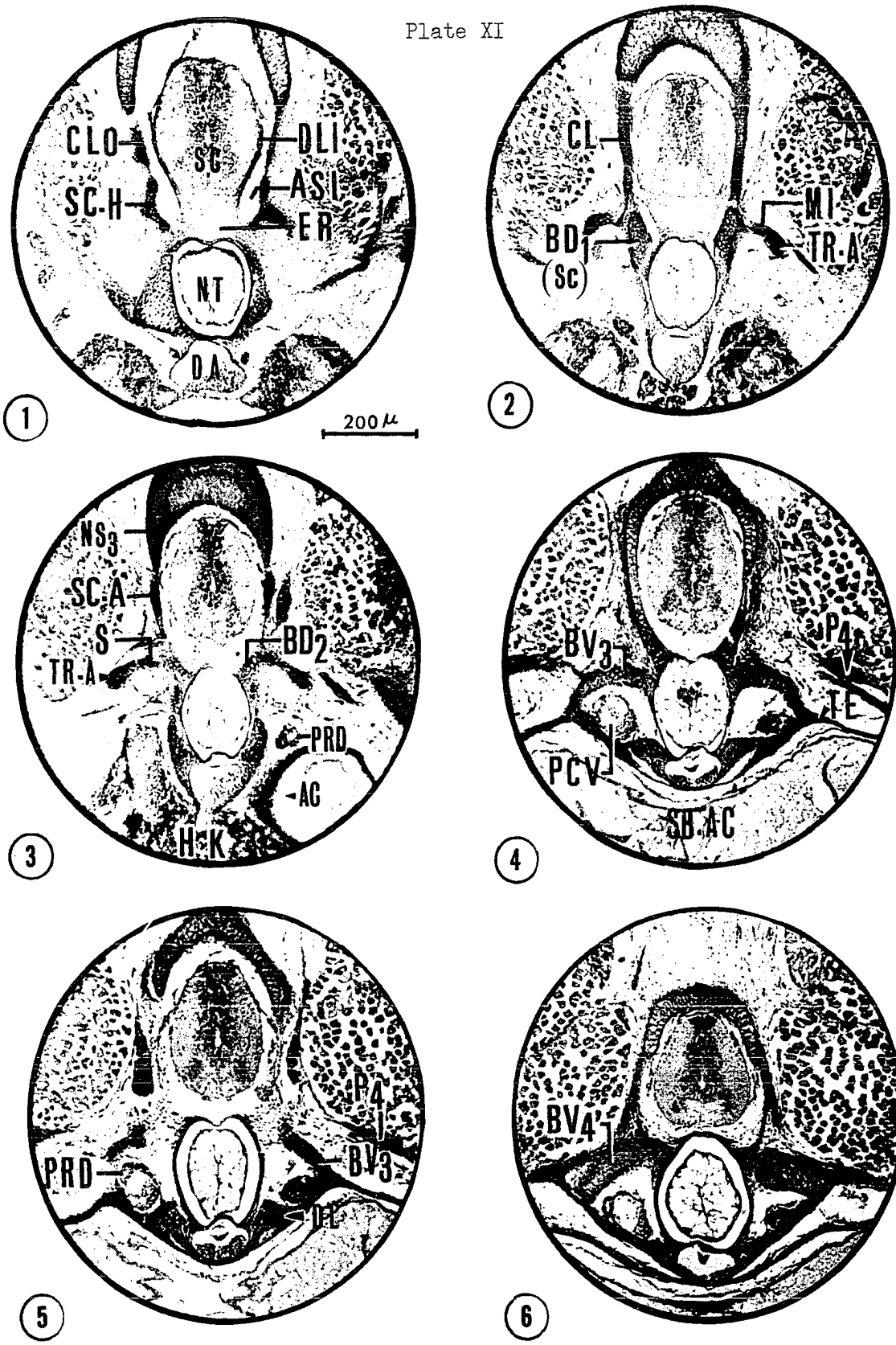
Fig. 3 - Transverse section showing the basidorsals of the second vertebra, posterior to the section in Fig. 2. Note the manubrium incudis.

Fig. 4 - Transverse section showing the basidorsals and basiventrals of the third vertebra, posterior to the section of Fig. 3. Note the pleural rib of the fourth vertebra which is going to form the fourth parapophysis.

Fig. 5 - Transverse section showing the distal portion of the third basiventral, posterior to the section of Fig. 4.

Fig. 6 - Transverse section showing the basiventrals of the fourth vertebra posterior to the section in Fig. 5. Note that the pleural rib joins the dorsodistal portion of each basiventral.

Plate XI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AC
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BV3
P4
TE
PCV
SB-AC
4
PRD
P4
BV3
DL
5
BV4
6

Plate XII

All the frontal sections are photographed as if viewed from the dorsal surface; therefore, the right side of the larva is at the reader's right.

Fig. 1 - Frontal section showing the basidorsals of the third and the fourth vertebrae of a 245-hr, 13.7-mm larva. Note the additional spinal ganglion and the other spinal ganglia.

Fig. 2 - Frontal section showing the basidorsals of the first, third, and fourth vertebrae below the section of Fig. 1. Note the horizontal process of the scaphium and the atrium sinus imparis on each side of the endorhachis.

Fig. 3 - Frontal section showing the first four basidorsals of the first four vertebrae below the section of Fig. 2. Note the manubrium incudis of the intercalarium.

Fig. 4 - Frontal section, below the section of Fig. 3, showing the origins of the manubrium incudis and the parapophysis of the fourth vertebra.

Fig. 5 - Frontal section, below that of Fig. 4, showing the first future vertebra and the origin of the anterior process of the tripus. Note the interbasiventral ligament and the interossicular ligament.

Fig. 6 - Frontal section, below that in Fig. 5, showing the ductus endolymphaticus, sinus endolymphaticus and sinus imparis in relation with the first future vertebra.

Plate XII

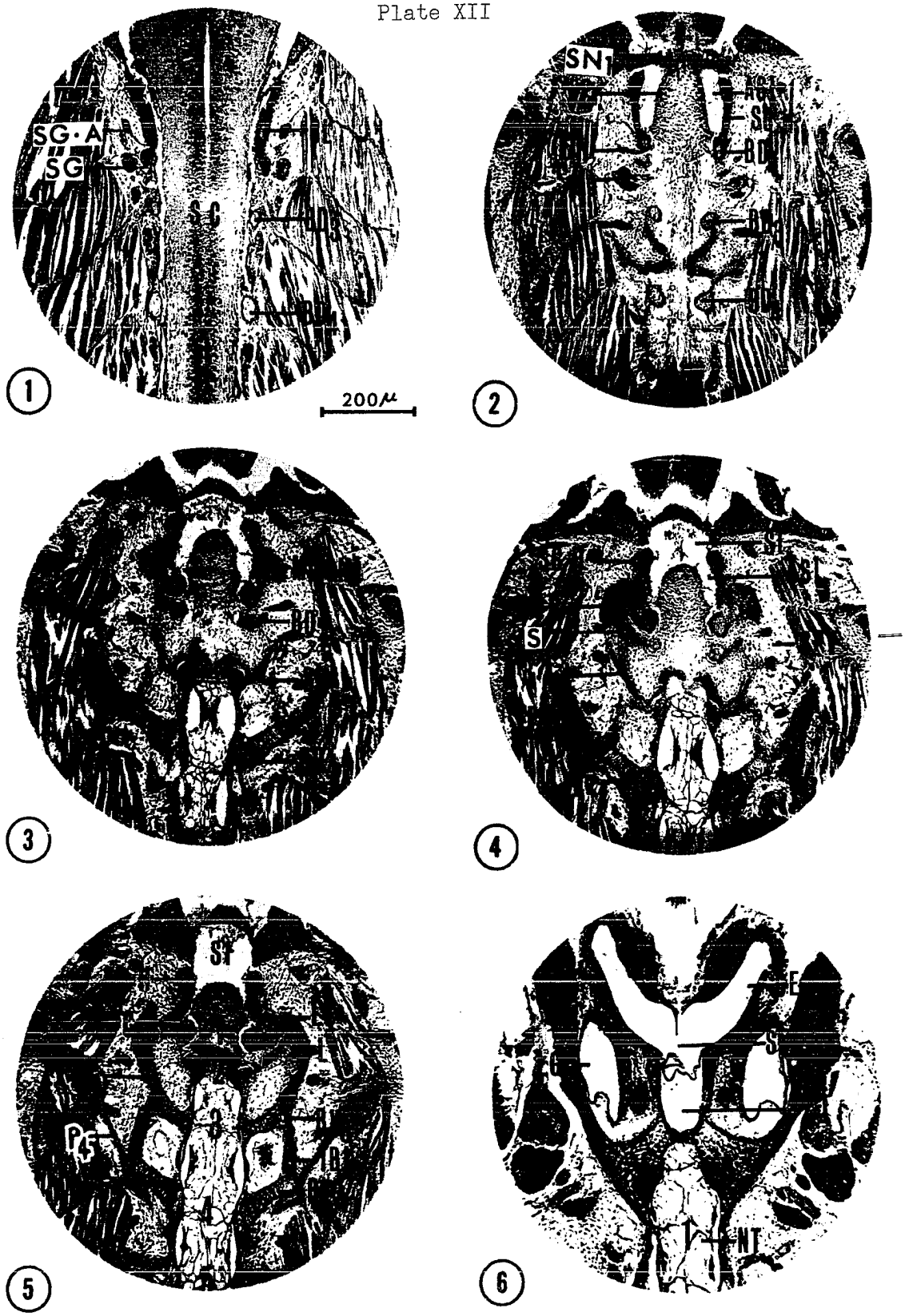


Plate XIII

All the transverse sections are photographed as if viewed from the cephalic surface; therefore, the right side of the larva is at the reader's left.

Fig. 1 - Transverse section showing the horizontal process of the scaphium and the sinus imparis of a 346-hr, 15.7-mm larva.

Fig. 2 - Transverse section, posterior to that of Fig. 1, showing the endorhachis, atrium sinus imparis, horizontal process of the scaphium, ligamentum scaphium, and the manubrium incudis.

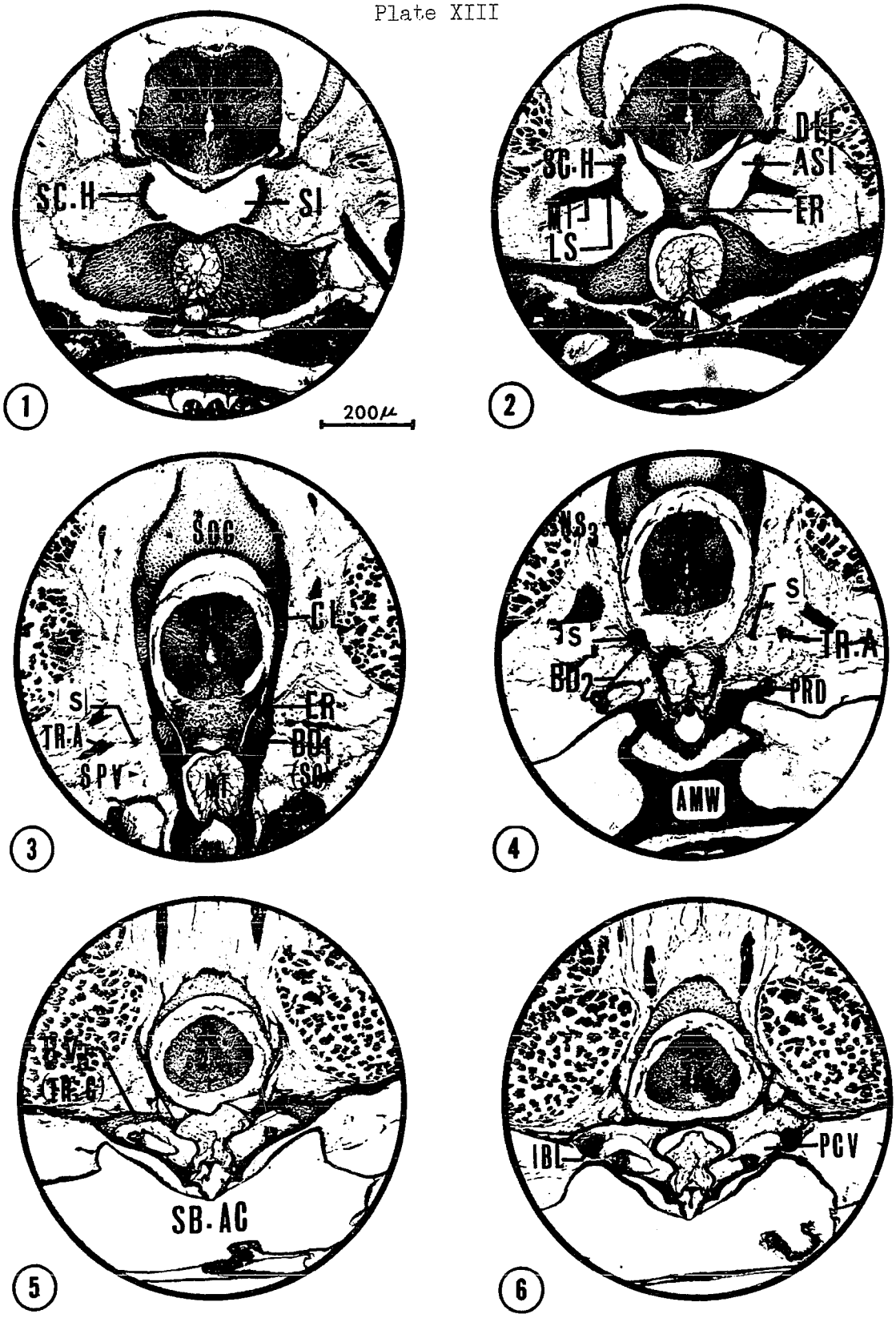
Fig. 3 - Transverse section, posterior to that of Fig. 2, showing the basidorsals of the first future vertebra and the claustra. Note the anterior process of the tripus.

Fig. 4 - Transverse section, posterior to that of Fig. 3, showing the basidorsal of the second future vertebra and the shaft of the intercalarium.

Fig. 5 - Transverse section, posterior to that of Fig. 4, showing the basiventrals of the third vertebra.

Fig. 6 - Transverse section, posterior to that in Fig. 5, showing the interbasiventral ligament.

Plate XIII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PRD
AMW
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BD
TR.C
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5
IBL
PCV
6

Plate XIV

All the transverse sections are photographed as if viewed from the cephalic surface; therefore, the right side of the alevin is at the reader's left.

Fig. 1 - Transverse section showing the ossified portion of the claustrum, horizontal process of the scaphium, intercalarium and the anterior process of the tripus of a 36.0-mm alevin. Note the ligamentum scaphium and the ligamentum tripus.

Fig. 2 - Transverse section, posterior to that of Fig. 1, showing the claustrum, the endorhachis, and the interossicular ligament.

Fig. 3 - Transverse section, posterior to that of Fig. 2, showing the saccus paravertebralis.

Fig. 4 - Transverse section, posterior to that of Fig. 3, showing the ascending and condylar processes of the scaphium. Note the disappearance of the shaft of the intercalarium, which is usually located between the anterior process of the tripus and the horizontal process of the scaphium.

Fig. 5 - Transverse section, posterior to that of Fig. 4, showing the interbasiventral ligament between the articular process of the tripus and the parapophysis of the fourth vertebra.

Fig. 6 - Transverse section, posterior to that of Fig. 5, showing the crescentic process of the tripus and the dorsal lamina.

Plate XIV

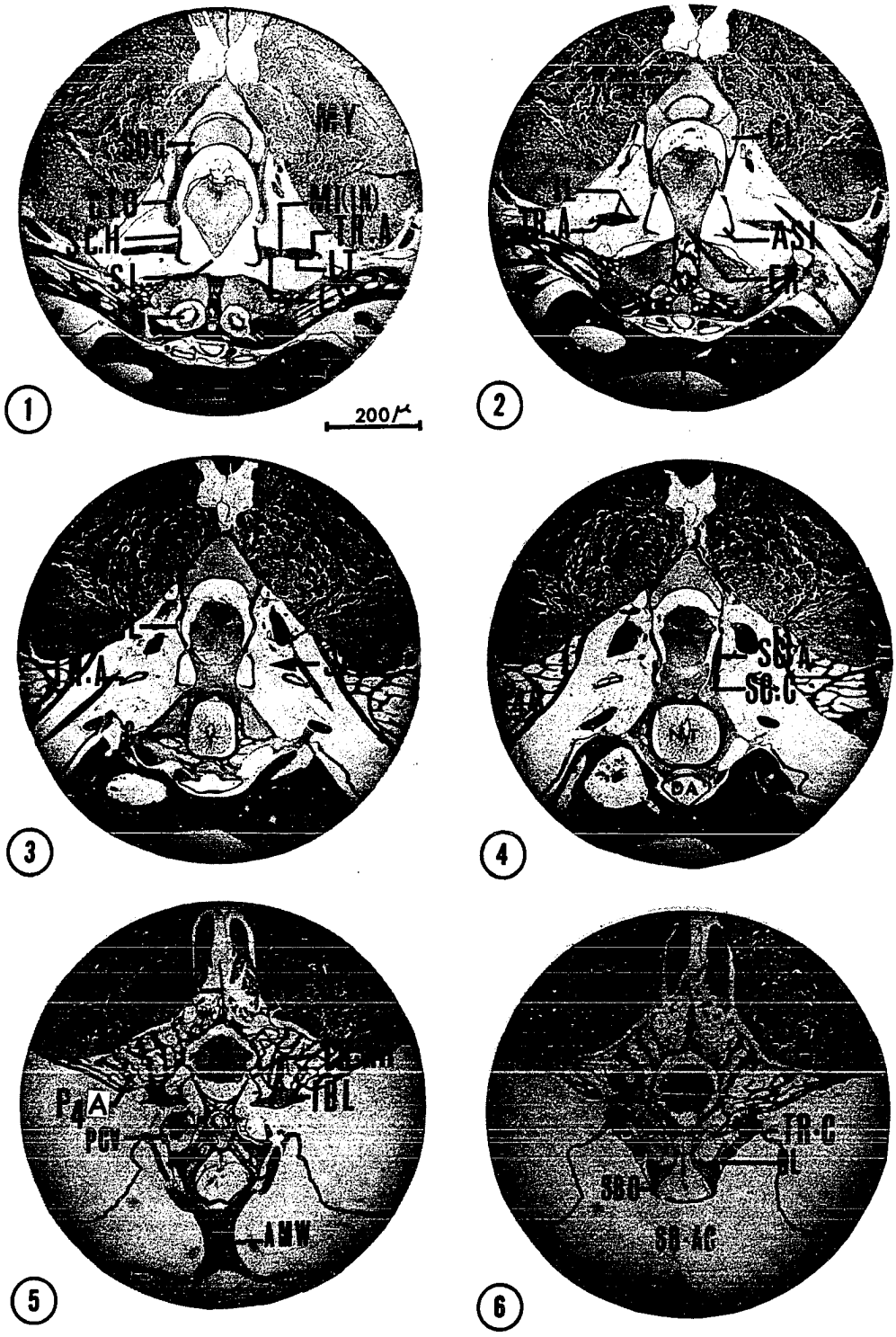


Plate XV

Fig. 1 - Frontal section through the notochord of a 123-hr, 9.5-mm larva, showing the vacuolated and peripheral notochordal cells.

Fig. 2 - Transverse section through the future vertebral region of a 123-hr, 9.5-mm larva.

Fig. 3 - Transverse section through the future intervertebral region posterior the section of Fig. 2. Note that, in this stage, this region is not readily distinguished from the vertebral region of Fig. 2.

Fig. 4 - Frontal section through the notochord of a 158-hr,10.7-mm larva, showing the thickened peripheral notochordal cells and the perichordal sheath cells in the future intervertebral regions.

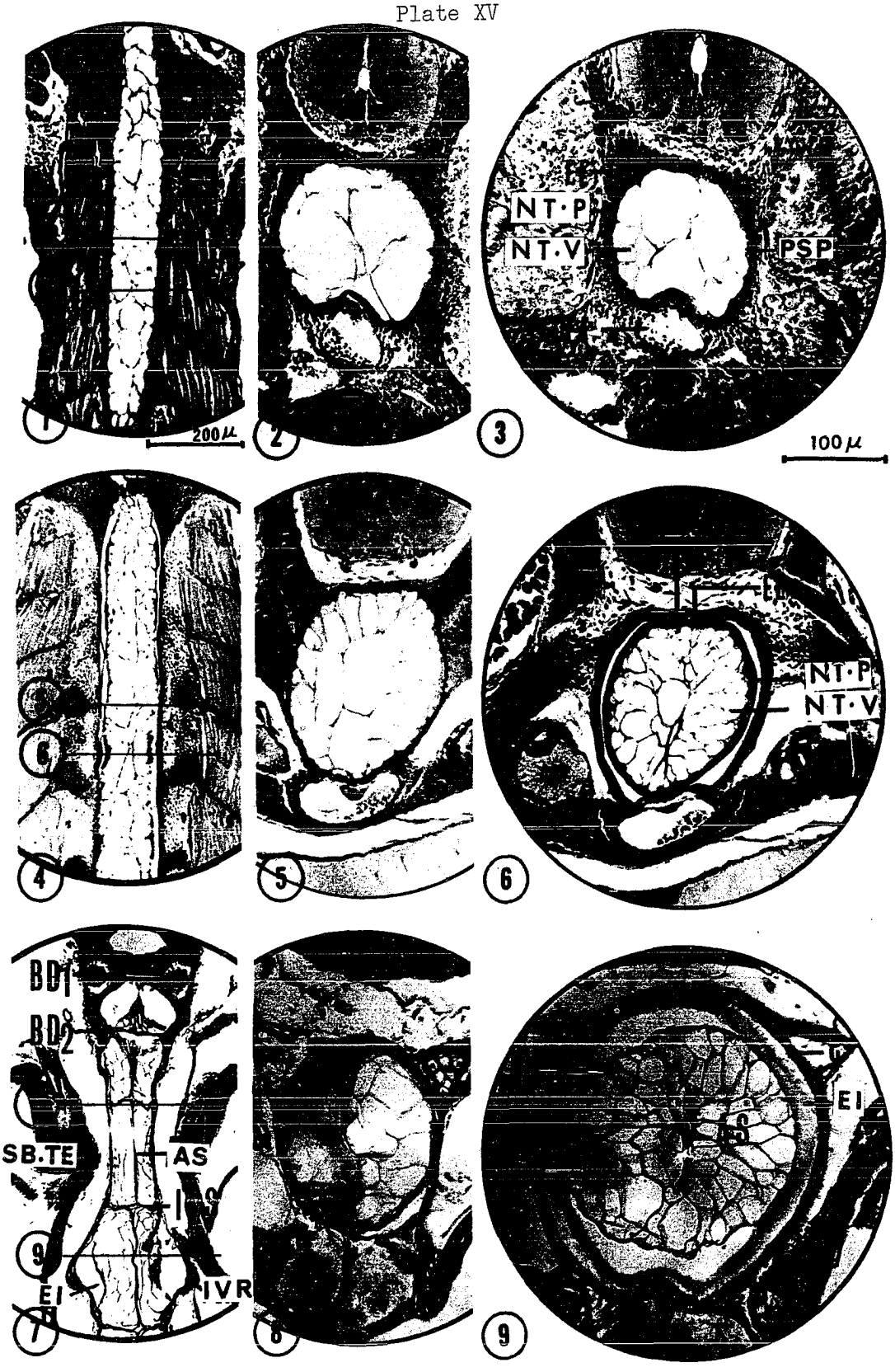
Fig. 5 - Transverse section through the future vertebral region of a 218-hr,12.7-mm larva.

Fig. 6 - Transverse section through the future intervertebral region posterior to the section of Fig. 5.

Fig. 7 - Frontal section through the notochord of a 517-hr,19.2-mm larva, showing the first clearly evident signs of the reduction of the intervertebral regions between the second and third and the third and fourth future vertebrae resulting in their eventual coalescence.

Fig. 8 - Transverse section through the future vertebral region of a 595-hr,20.0-mm larva.

Fig. 9 - Transverse section through the future intervertebral region of a 595-hr,20.0-mm larva.


200 μ
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NT·V
PSP
100 μ
NT·P
NT·V
BD1
BD2
SB.TE
AS
EI
IVR
EI

THE MORPHOLOGY OF THE SWIM BLADDER IN THE ADULT AND ITS DEVELOPMENT

(Abbreviations)

AC	- Anterior chamber of the swim bladder
B	- Brain
BD 1-4	- Basidorsals of the 1st through the 4th vertebrae
BV 3-5	- Basiventrals of the 3rd through the 5th vertebrae
CAP	- Capillaries
CC	- Complex vertebra
CM	- Circular striated muscles
DA	- Dorsal aorta
DP	- Dorsal peritoneum
EPI	- Epithelium
ESO	- Esophagus
FG	- Foregut
FM (ITI)	- Foamy matrix (intertunica interna)
HK	- Head kidney
IBL	- Interbasiventral ligament
ICA	- Interchamber aperture
IL	- Interossicular ligament
IT	- Intertunic layer
K	- Kidney
LCA	- Lateral cutaneous area
LIV	- Liver
LM	- Longitudinal striated muscles
LS	- Longitudinal septum
LS.P	- Longitudinal septum primordium
LU	- Lumen of the swim bladder
MG	- Midgut
MG(S)	- Midgut (stomach)
MMC	- Migrating mesenchymal cells
NA_3	- Neural arch of the third vertebra
NT	- Notochord
PA	- Pancreas
P_4	- Pleural rib of the fourth vertebra
PC	- Posterior chamber of the swim bladder
PD	- Pneumatic duct
PRD	- Pronephric duct
RF	- Radial fibers
RN	- Radial nodules
SB	- Swim bladder

SB.AC - Anterior chamber of the swim bladder
SB.D - Swim bladder diverticulum
SB.P - Swim bladder primordium
SB.PC - Posterior chamber of the swim bladder
SB.PE - Posterior end of the swim bladder
SC - Scaphium
SG - Spinal ganglia
SOM (TE) - Somatic mesoderm (tunica externa)
SPM - Splanchnic mesoderm
TE - Tunica externa
TI - Tunica interna
TR.A - Anterior process of the tripus
TR.C - Crescentic process of the tripus
TS - Transverse septum
TS.P - Transverse septum primordium
Y - Yolk
1-5 - 1st through 5th centra

Plate XVI

Fig. 1 - Lateral view of Ictalurus punctatus. Note the lateral cutaneous area.

Fig. 2 - Ventral view of the swim bladder with the pneumatic duct.

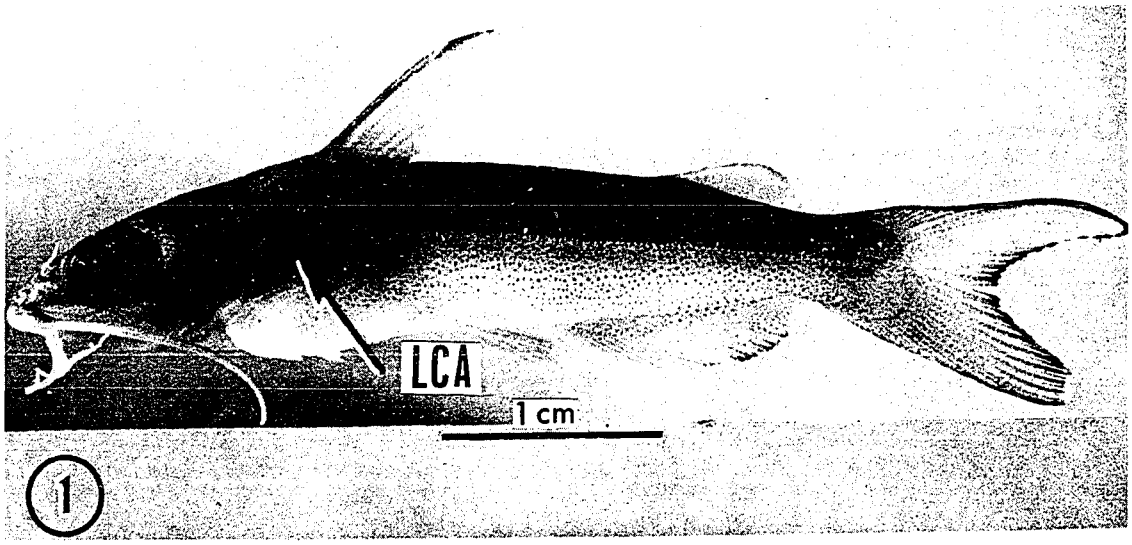
Fig. 3 - Ventral view of the interior of the swim bladder, in situ, after cutting the ventral wall.

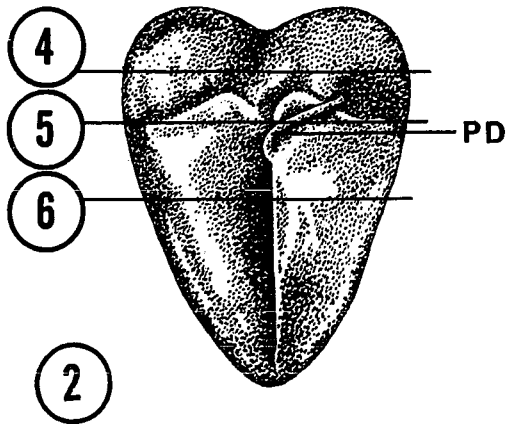
Fig. 4 - Transverse section through the anterior chamber of the swim bladder.

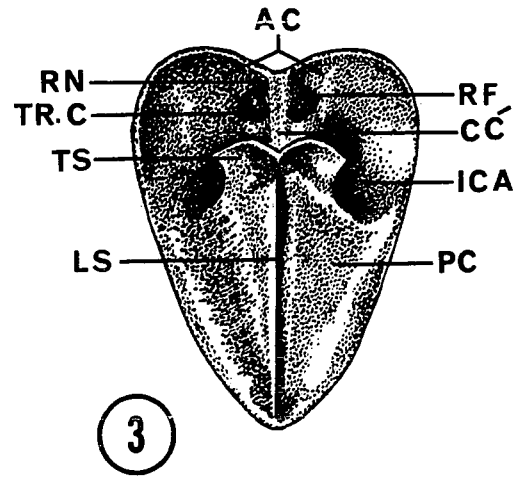
Fig. 5 - Transverse section through the transverse septum and the interchamber apertures of the swim bladder.

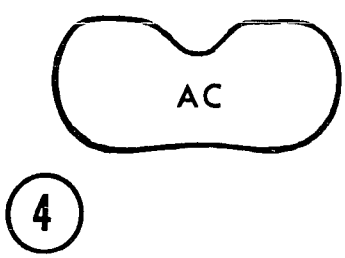
Fig. 6 - Transverse section through the longitudinal septum and the two posterior chambers of the swim bladder.

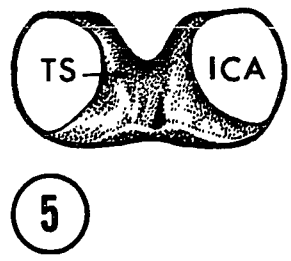
Plate XVI











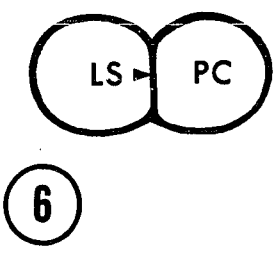


Plate XVII

The anterior end of all sagittal sections is at the reader's left.

All the transverse sections are photographed as if viewed from the cephalic surface; therefore, the right side of the larva is at the reader's left.

Fig. 1 - Sagittal section showing the swim bladder and the pneumatic duct of a 127-hr, 9.7-mm larva. Numbered lines indicate levels of transverse sections, Figs. 2-4.

Fig. 2 - Transverse section showing the swim bladder diverticulum arising from the right dorsolateral side of the foregut of a 110-hr, 8.3-mm larva.

Fig. 3 - Transverse section showing that the primitive swim bladder is still below the level of the dorsal peritoneum. This section is posterior to the section of Fig. 3.

Fig. 4 - Transverse section showing the posterior portion of the swim bladder diverticulum, posterior to the section of Fig. 3.

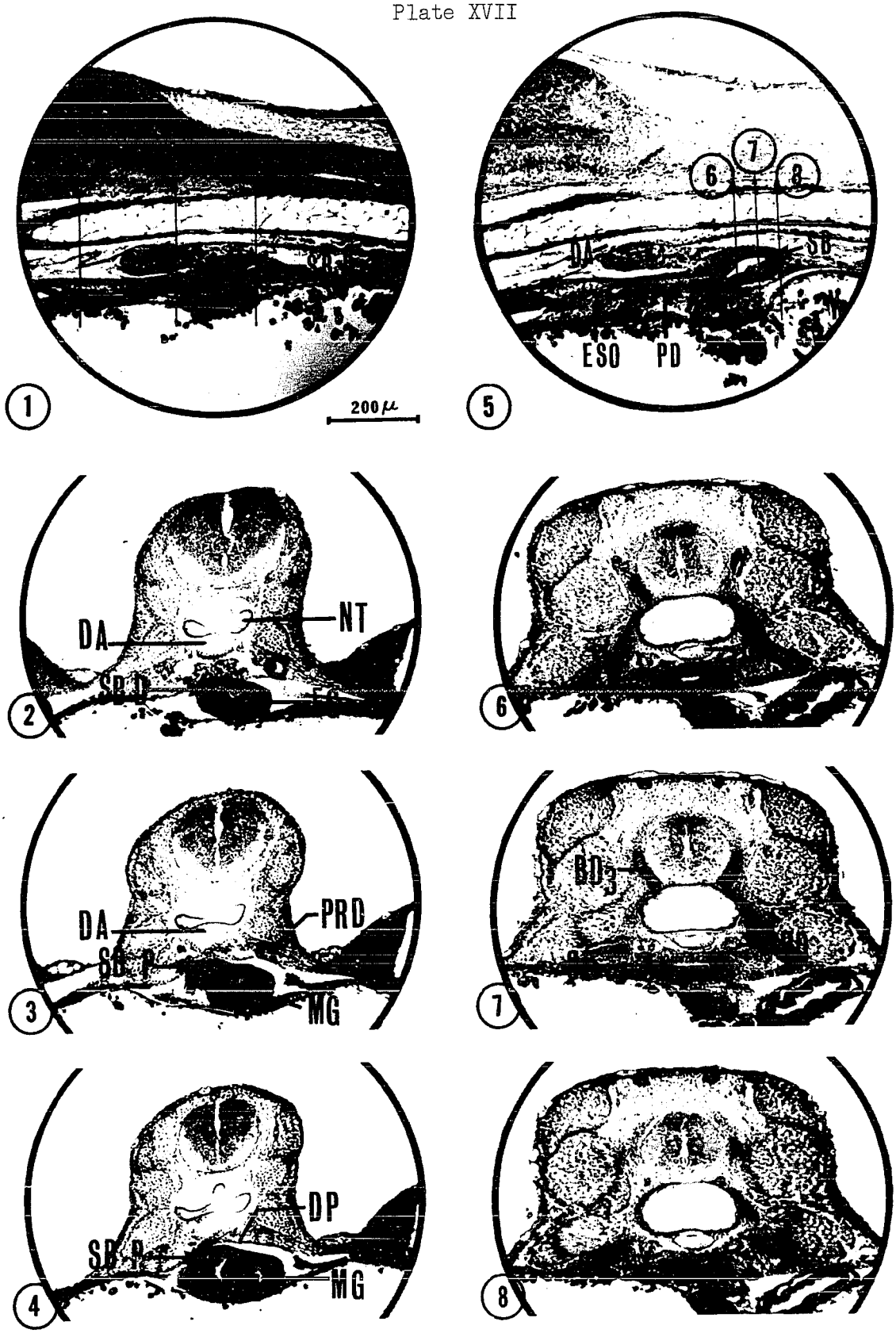
Fig. 5 - Sagittal section showing the primitive swim bladder and the pneumatic duct of a 146-hr, 10.0-mm larva. Note the junction of the pneumatic duct with the anterior portion of the swim bladder. Numbered lines indicate levels of transverse sections, Figs. 6-8.

Fig. 6 - Transverse section showing the primitive swim bladder near the entrance of the pneumatic duct of a 152-hr, 10.4-mm larva.

Fig. 7 - Transverse section showing the middle portion of the primitive swim bladder, posterior to the section of Fig. 6.

Fig. 8 - Transverse section showing the posterior portion of the swim bladder, posterior to the section of Fig. 7.

Plate XVII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DP
SP.D
MG
8
SG

Plate XVIII

The anterior end of all sagittal sections is at the reader's left.

All the transverse sections are photographed as if viewed from the cephalic surface; therefore, the right side of the larva is at the reader's left.

Fig. 1 - Sagittal section showing the swim bladder and the pneumatic duct of a 152-hr, 10.4-mm larva. Note that the pneumatic duct opens into the anteroventral portion of the swim bladder. Numbered lines indicate levels of transverse sections, Figs. 2-4.

Fig. 2 - Transverse section showing the anterior portion of the swim bladder of a 170-hr, 11.1-mm larva. Note the entrance of the pneumatic duct into the anteromidventral portion of the swim bladder.

Fig. 3 - Transverse section through the middle portion of the swim bladder showing the coalescence of the midventral portion of the endodermal epithelium with that of the middorsal portion of the same layer and the formation of the two posterior chambers. This section is posterior to the section of Fig. 2.

Fig. 4 - Transverse section showing the local thickening in the posteromidventral portion of the condensed somatic mesodermal layer. This section is posterior to the section of Fig. 3.

Fig. 5 - Sagittal section showing the swim bladder and the pneumatic duct of a 185-hr, 11.7-mm larva. Note the vertical entrance of the pneumatic duct into the anteromidventral portion of the swim bladder.

Fig. 6 - Transverse section showing the anterior portion of the swim bladder of a 182-hr, 11.5-mm larva. Note the entrance of the pneumatic duct.

Fig. 7 - Transverse section showing the middle portion of the swim bladder posterior to that in Fig. 6. Note the dorsal growth of the midventral thickening of the tunica externa and the formation of the two parallel posterior chambers.

Fig. 8 - Transverse section showing the posterior portion of the swim bladder posterior to that in Fig. 7. Note the complete formation of the longitudinal septum.

Plate XVIII

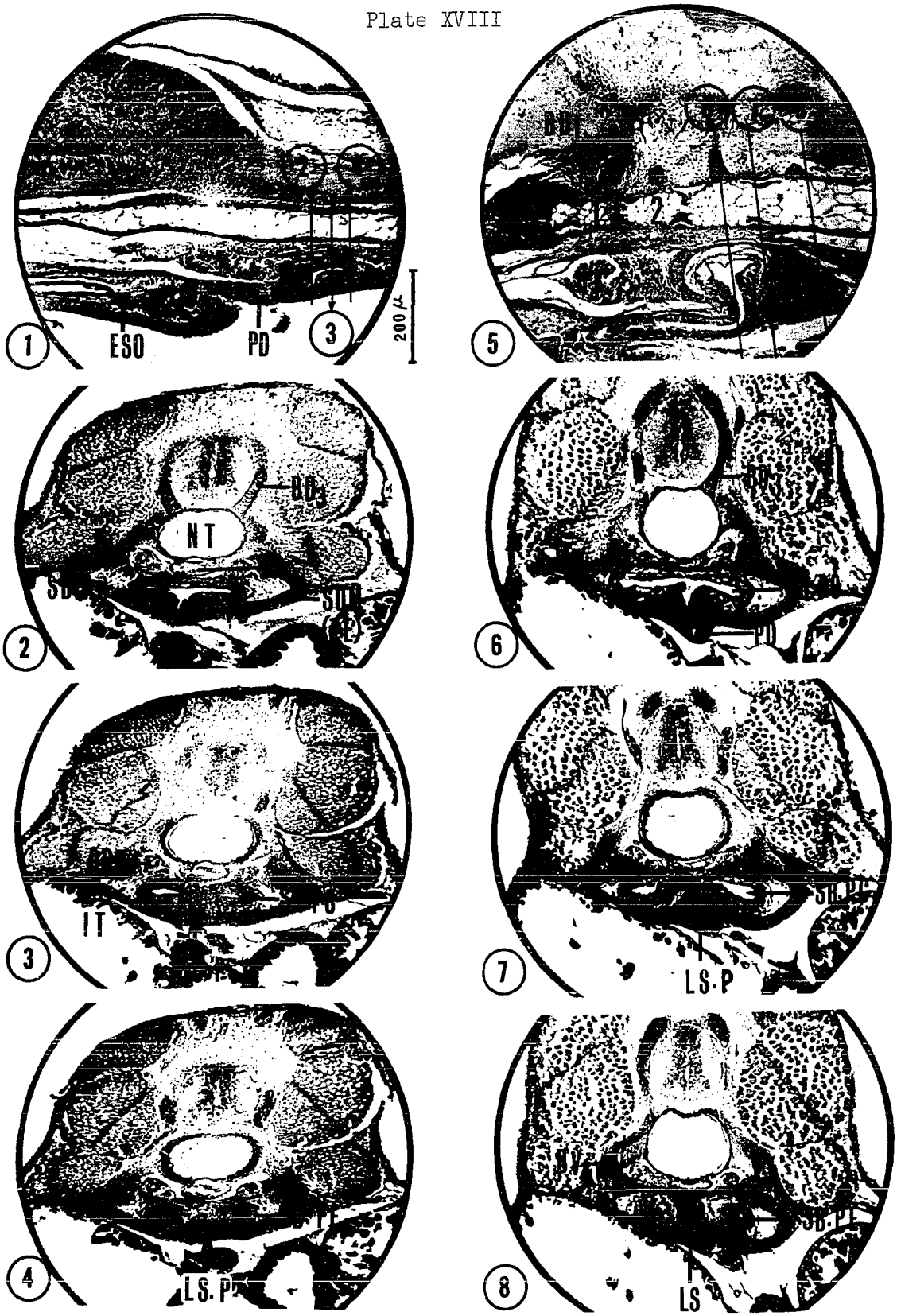


Plate XIV

The anterior end of the sagittal section is at the reader's left.

All the frontal sections are photographed as if viewed from the dorsal surface, therefore, the right side of the larva is at the reader's right.

Fig. 1 - Sagittal section showing the swim bladder and the pneumatic duct of a 206-hr, 12.4-mm larva. Note the U-shape of the pneumatic duct, the large anterior chamber, and the longitudinal septum. Numbered lines indicate levels of the frontal sections, Figs. 2-6.

Fig. 2 - Frontal section showing the swim bladder of a 200-hr, 12.3-mm larva. Note the layers of the swim bladder wall, the longitudinal septum, and the migrating somatic mesodermal cells.

Fig. 3 - Frontal section through the swim bladder below the section of Fig. 2. Note the layers of the swim bladder wall, the cells in the foamy matrix and the longitudinal septum.

Fig. 4 - Frontal section through the swim bladder below the section of Fig. 3. Note the primordium of the transverse septum which is anterolateral to the longitudinal septum. Note also the opening of the pneumatic duct and the capillaries in the foamy matrix.

Fig. 5 - Frontal section through the esophagus and the pneumatic duct of another 200-hr, 12.3-mm larva, below the section of Fig. 4.

Fig. 6 - Frontal section through the esophagus-stomach junction, below the section of Fig. 5. Note the pneumatic duct arising from the dorsolateral right side of the esophagus just anterior to the stomach. Note also the inner, longitudinal, striated muscles and the outer, circular, striated muscles of the esophagus.

Plate XIX

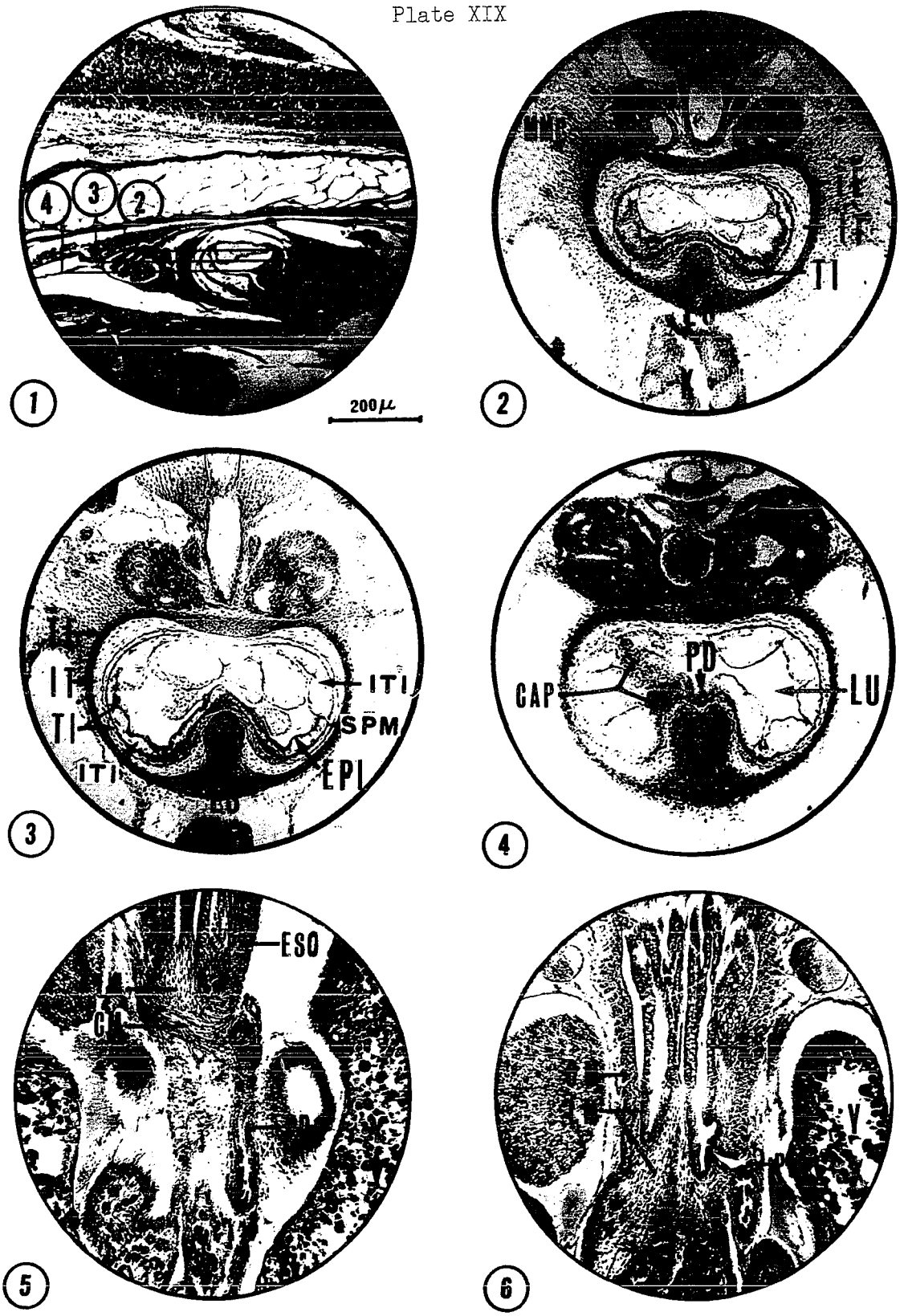


Plate XX

The anterior end of all sagittal sections is at the reader's left.

All the transverse sections are photographed as if viewed from the cephalic surface; therefore, the right side of the larva is at the reader's left.

Fig. 1 - Sagittal section through the anterior and posterior chambers of the swim bladder and the proximal portion of the pneumatic duct of a 224-hr, 13.0-mm larva. Note the layers in the swim bladder wall, the pneumatic duct-esophagus junstion, the basiventrals of third and fourth vertebrae and the interbasiventral ligament between them.

Fig. 2 - Sagittal section through the swim bladder and the distal portion of the pneumatic duct medial to the section of Fig. 1. Note the interossicular ligament. Numbered lines indicate levels of transverse sections, Figs. 4-6.

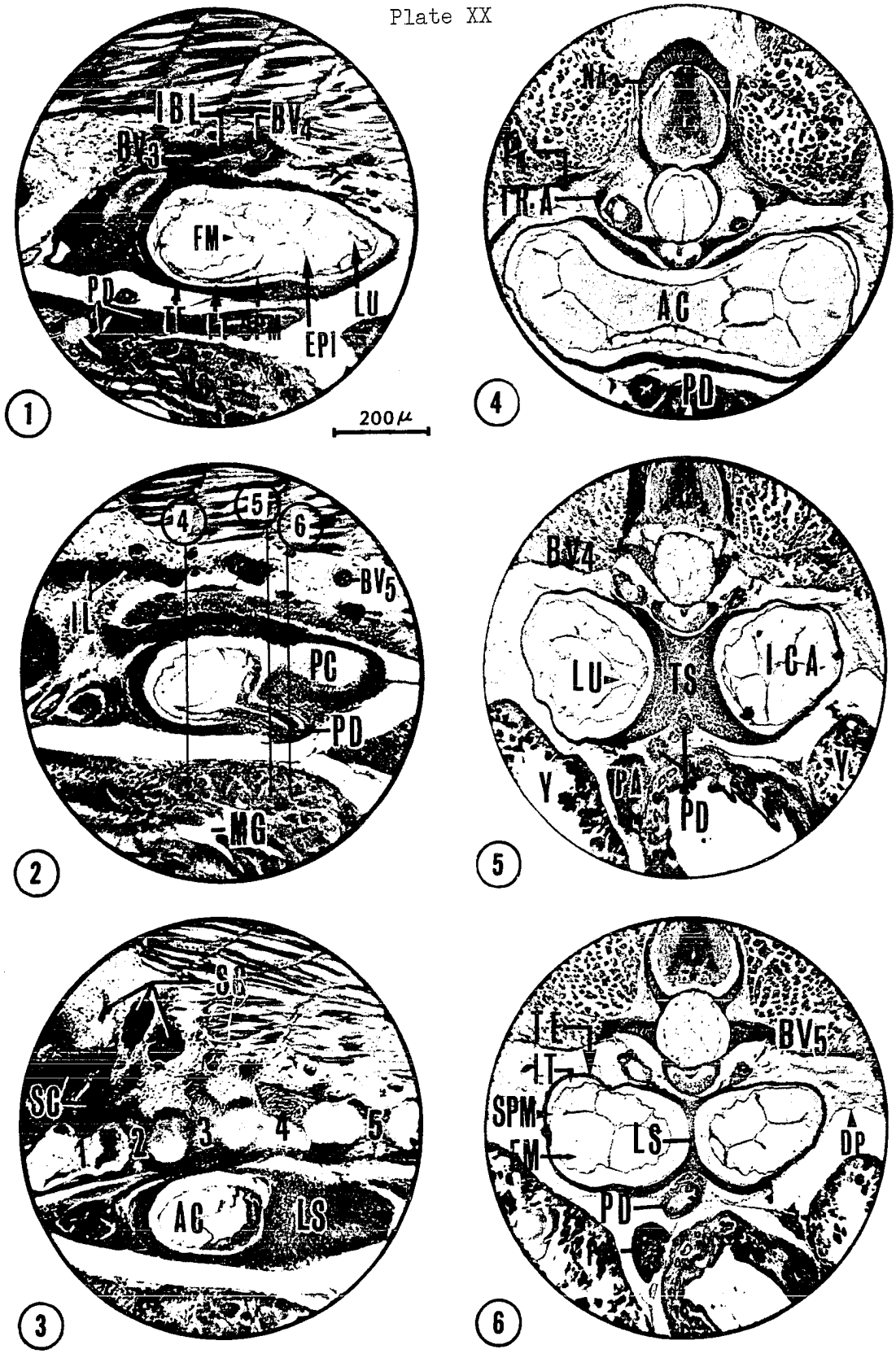
Fig. 3 - Midsagittal section through the anterior chamber and the longitudinal septum of the swim bladder. Note the length of the swim bladder in relation to the number of vertebra above it.

Fig. 4 - Transverse section through the anterior chamber of the swim bladder of a 237-hr, 13.5-mm larva. Note the foamy matrix.

Fig. 5 - Transverse section through the transverse septum posterior to the section of Fig. 4. Note that the pneumatic duct is cut twice.

Fig. 6 - Transverse section through the longitudinal septum posterior to the section of Fig. 5. Note the layers of the swim bladder and the section of the pneumatic duct near its curvature.

Plate XX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PD
MG
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SC
SC
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AC
LS
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IL
BV5
SPM
FM
LS
DP
PD
6

Plate XXI

All the transverse sections are photographed as if viewed from the cephalic surface; therefore, the right side of the larva is at the reader's left.

Fig. 1 - Transverse section through the anterior chamber of the swim bladder between the third and fourth vertebrae of a 263-hr, 14.0-mm larva. Note the layers of the swim bladder wall, and the foamy matrix between the epithelial layer and the splanchnic mesodermal layer.

Fig. 2 - Transverse section through the anterior chamber of the swim bladder at the same level of the section of Fig. 1 but from a 283-hr, 14.2-mm larva. Note the disappearance of the foamy matrix on the right side and the appearance of the lumen of the swim bladder probably filled with gas in this stage.

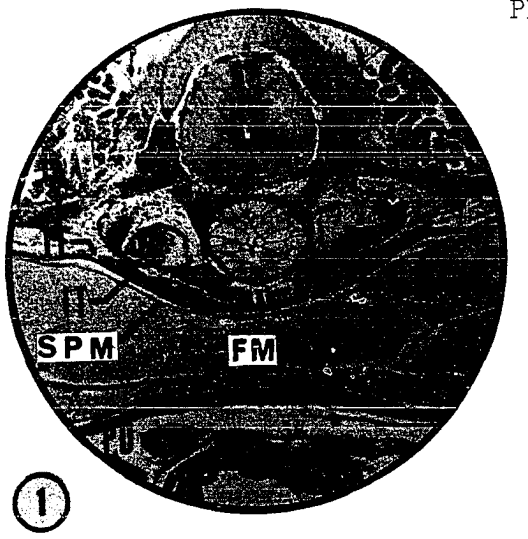
Fig. 3 - Transverse section through the anterior chamber of the swim bladder at the same level as the section of Figs. 1 and 2, but from a 336-hr, 15.6-mm larva. Note the disappearance of the foamy matrix and the fully formed appearance of the lumen of the swim bladder.

Fig. 4 - Transverse section through the anterior chamber of the swim bladder of a 457-hr, 17.0-mm larva. Note that the intertunic layer has disappeared and that the lumen of the swim bladder has increased. Note also the lateral cutaneous areas, and the origin of the pneumatic duct from the dorsolateral right side of the esophagus.

Fig. 5 - Transverse section through the transverse septum, posterior to the section of Fig. 4. Note the two cross sections through the pneumatic duct and the interchamber aperture.

Fig. 6 - Transverse section through the two posterior chambers posterior to the section of Fig. 5. Note the longitudinal septum.

Plate XXI



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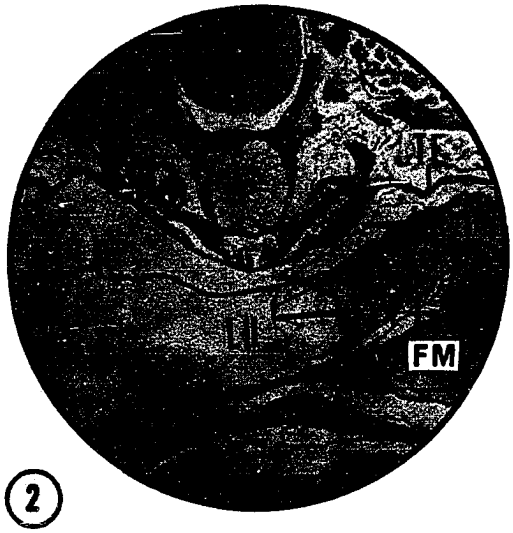

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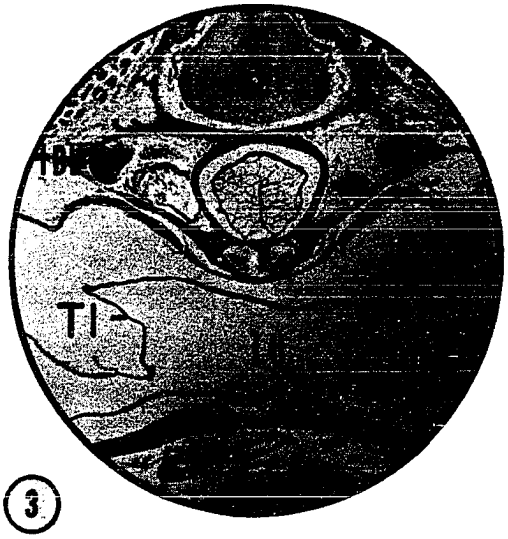

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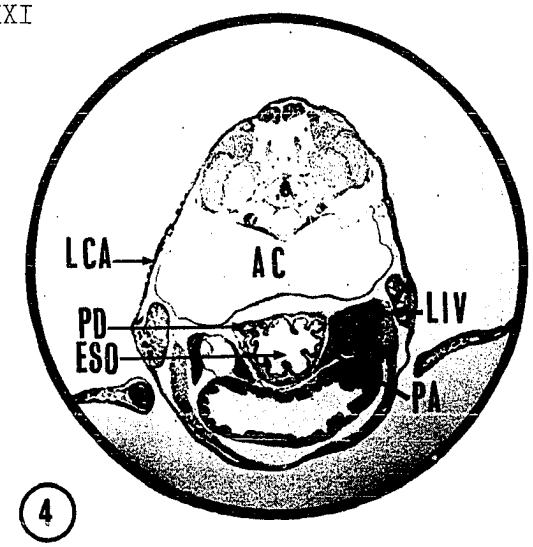

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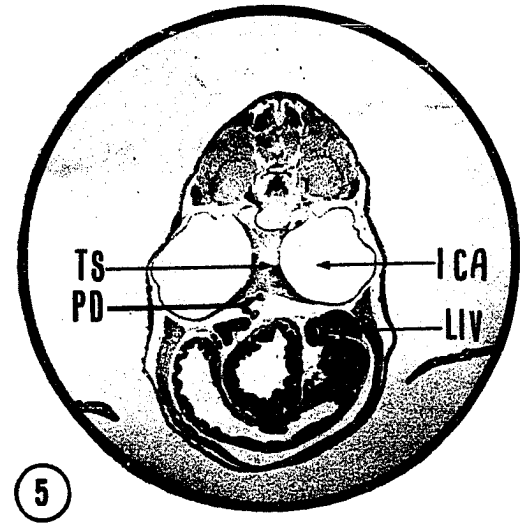

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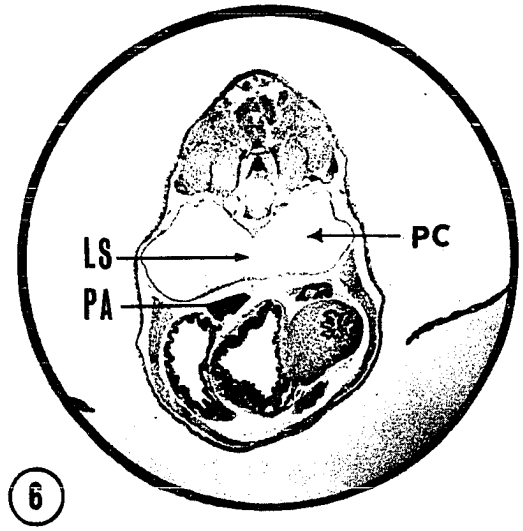

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